

SEASONAL MIGRATION OF MULE DEER

A DISSERTATION SUBMITTED IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY IN
THE UNIVERSITY OF MICHIGAN

By
CARL PARCHER RUSSELL

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SEASONAL MIGRATION OF MULE DEER

INTRODUCTION

True seasonal migrations of animals bring about changes of range. They periodically recur and alternate in direction. Such movements are known among crustaceans, fishes, reptiles, birds, and mammals (Cahn, 1925; Coward, 1912; Meek, 1916). Long before the Christian Era, the problem of bird migration was a subject of speculation among philosophers, and through the ages the matter has found place in the literature of many lands (Wetmore, 1926). Today, after many workers have given attention to the problem, it is yet impossible to be sure which causative factors are responsible for the remarkable seasonal movements of birds (Wetmore, 1926).

The migratory habits of the mule deer, *Odocoileus hemionus*, have been noted in the writings of explorers and naturalists since the first noteworthy reference to the species by Lewis and Clark in 1814 (Thwaites, 1904). The first printed mention of the species was that of Edward Umfreville, 1789. Migration, however, has been accepted as a commonplace habit by which the mule deer, like other migratory species, gains certain advantageous ends, and, to the best of the writer's knowledge, no attempt has been made to inquire into the causative factors in the seasonal movements, nor has the biological significance of the migration ever received consideration. The question as to *why* a species habitually migrates constitutes a problem in ecology that challenges any one who inquires into the philosophical aspects of field natural history, and in the present study it would appear that the problem is subject to attack by practical methods which are productive of concrete results.

Twice each year the herds of mule deer of the mountains of the western United States change their range. Their winter habitat comprises favored valleys and slopes three thousand to six thousand feet above sea level. In the spring, the greater number of the animals leave their winter homes and climb to higher valleys and plateaus. This movement may involve a climb of five or six thousand feet and travel over a horizontal distance of fifty miles. Seton (1927) calls attention to a Colorado locality where the drift involves travel over a 150 mile route. In the fall, the movement is reversed. The area occupied in winter is referred to as the *winter range*, and the territory in which the summer is spent as the *summer range*. Lanes of travel between the two are *migration routes*. The migration itself is commonly referred to as the *drift*.

It is the purpose of this paper to point out the details of mule deer migrations, to describe the correlation of these movements with other phases of the animal's life history and with periodic physical phenomena, and to demonstrate that definite facts are available which are subject to interpretation.

METHODS OF STUDY

In 1923, the writer assumed the duties of park naturalist in Yosemite National Park. Exceptional opportunities for study of the life history of the mule deer of the region encouraged an immediate undertaking of field work. The study was pursued in connection with official duties and continued through a part of 1928. In the summer of 1928, the writer was transferred to Yellowstone National Park, Wyoming, and he took advantage of the opportunity to continue study of the mule deer in that region. The same general procedure was followed for another three years, and a careful comparison of habits and movements was made for the two regions, the central Sierra Nevada and the Yellowstone section of the Rocky Mountains. Residence in Yosemite National Park was continuous from June, 1923 to July, 1928. The Yellowstone studies were limited to seven months of each year, but they are representative of all seasons and adequate for comparison with the Yosemite findings.

Field work was not spasmodic but was carried on daily or at intervals of a day or two. Food plants were collected after deer were observed to partake of them, and the specimens were identified by the writer or submitted to specialists for identification. In Yellowstone, Dr. W. B. McDougal assisted. In Yosemite, the park botanist, Mrs. Enid Michael, aided in this work. The herbaria of the Yellowstone Museum and the Yosemite Museum were most helpful in the undertaking. Stomach contents were examined in the laboratories of the Yosemite Museum and the Yellowstone Museums. During the slaughter of the northern herd of Yosemite deer, because of the epidemic of foot and mouth disease, 1924-1925 (Mohler, 1926), many stomachs were given cursory examinations in the field.

All life zones and ecological situations received full consideration. In Yosemite, the entire park was given careful study, and outlying regions to a distance of thirty to fifty miles were included. The entire range of the Yosemite deer herds was under observation. Regions not penetrated by roads were visited with pack outfits. The Yosemite road system is good, and the use of an automobile greatly facilitated field work. In winter, the upper reaches of the park were inaccessible to automobiles, and trips were made on snowshoes or skis. In Yellowstone, all of the park was studied with the exception of the southeast corner. In this park, too, a comprehensive system of roads made possible the study of large areas at frequent intervals. Some regions inaccessible to automobiles were visited on foot or in the saddle.

ACKNOWLEDGMENTS

The extensive territory*involved in the Yellowstone study necessitated wide coöperation from a small army of national park and national forest employees. It was possible to secure the cordial interest of the supervisors of

nine national forests, and it is to be acknowledged that without their assistance results here presented would necessarily have been limited to areas much smaller than those actually covered in this treatment.

The following U. S. Forest Service officials have assisted by making special studies and reports or by placing results of their routine game studies at my disposal: Supervisors Roy Boothe, Inyo National Forest, Bishop, California; W. W. Maule, Mono National Forest, Minden, Nevada; J. R. Hall, Stanislaus National Forest, Sonora, California; R. T. Ferguson, Beartooth National Forest, Billings, Montana; J. N. Langworthy, Shoshone National Forest, Cody, Wyoming; S. W. Stoddard, Targhee National Forest, St. Anthony, Idaho; Acting Supervisor F. T. Carroll, Madison National Forest, Sheridan, Montana; Ranger E. P. White, Gallatin National Forest, Eldridge, Montana; and Range Examiner Arthur Cramer, Absaroka National Forest, Livingston, Montana.

In the course of much of the Yosemite work, I received the aid of George M. Wright, Assistant Park Naturalist. George Shedd of the Yosemite Park and Curry Company coöperated generously in making observations at Glacier Point (7200 ft.). Since leaving Yosemite, I have had many occasions to call on the Yosemite Museum staff for assistance. The Yellowstone National Park organization has developed a plan of wild life studies, results of which lent material aid in the present investigations. I am especially indebted to Chief Ranger George Baggeley; William Rush, in charge of elk study, and Dorr G. Yeager, park naturalist, for personally supporting my activities and arranging for the coöperation of some fifty Yellowstone park rangers and ranger-naturalists in making observations and reporting upon them. O. J. Murie of the United States Biological Survey and Superintendent Sam Woodwring of the Grand Teton National Park have given information on the movements of deer south of Yellowstone Park. W. T. Lathrop, meteorologist of the Yellowstone Weather Bureau Office, has given important assistance in supplying climatological data that were not available from published records. Other offices of the Weather Bureau have given coöperation, and published reports of that Bureau have been of prime importance in establishing some of the facts here presented. Dr. Lee R. Dice, Museum of Zoölogy, University of Michigan, has given of his time and interest in assisting through helpful criticism and suggestions during the preparation of this paper.

ROCKY MOUNTAIN MULE DEER OF YELLOWSTONE PARK

Yellowstone National Park is located in northwestern Wyoming, encroaching slightly upon Montana and Idaho. It contains some 3500 square miles of mountainous country, which saddles the backbone of the continent. The park center is a broad volcanic plateau approximately eight thousand feet above sea level. Surrounding it are mountain ranges with culminating peaks rising to ten and eleven thousand feet. North of the elevated plateau, the valley of the

Yellowstone drops to a level of five thousand three hundred feet. To the south, the lowest altitudes within the park are slightly higher than six thousand feet. In spite of the fact that the altitudinal variation is not great, Bailey (1930) has determined that a range of climate exists which includes four life zones. These are the Arctic-Alpine, Hudsonian, Canadian, and Transition. With the exception of the Arctic-Alpine Zone, this study of mule deer movements is concerned with all of the belts. Regions adjacent to the national park are largely national forest lands. They figure in this account, as shown on the accompanying map, because many of the park deer occupy winter ranges outside of the park boundaries.

OUTLINE OF HISTORY

The mule deer of the region are sturdy representatives of the species so frequently mentioned in the journals of Lewis and Clark (Thwaites, 1904), who in 1805-1806 observed them during their epochal journey across the northern end of the area with which this paper is concerned. The account of this exploration was not put in print until 1814. Charles Le Raye, an army man and adventurer of the early days of the Rocky Mountain fur trade, entered the Yellowstone region as a captive among Indian tribes in 1803. His journals (Cutler, 1812) provided the notes on mule deer which C. S. Rafinesque (1817) used as the basis for his description of the species. The type locality was "the Sioux River" (South Dakota).

Say (James, 1823) described a deer from "Major Long's Creek" (New Mexico) as *Cariacus macrotis*, and Caton (1876) used *Cervus macrotis californicus* as the name for a deer from "near Gaviota Pass, forty miles from Santa Barbara" (California). Merriam (1898) showed that *Odocoileus hemionus* was the specific name applicable for all of these deer. Bailey (1930) identifies the Yellowstone Park deer as *Odocoileus hemionus macrotis*, and Grinnell and Storer (1924) use *Odocoileus hemionus hemionus* for the Yosemite animal. No recent revision of the deer of this group has been made. It is probable that study will reveal subspecific differences not recognized at present, and for the purposes of this paper the name *Odocoileus hemionus* will therefore be used for Yellowstone and Yosemite animals alike.

SUMMER RANGE AND SUMMER ACTIVITIES

The 1930 game census taken by the ranger department of Yellowstone Park indicates a population of some 800 deer (Baggley, 1930). Most of these animals spend the summer on the central plateau. I have found no evidence that they travel higher than the 9000 foot level. Except for warm southwest exposures, timberline (upper edge of Hudsonian Zone) exists at about 9000 feet, and it is unlikely that deer often go above this belt. During the summer, deer are nowhere encountered in large herds. Two or three does with a spike buck, perhaps, may associate, but it is more common to find does

alone or with fawns of the year. Old bucks are usually alone but sometimes are accompanied by a younger male. Bucks are not frequently seen near the lanes of automobile travel but can be jumped from cover by searching higher slopes some few miles from roads, where favorable vegetation abounds.

REARING OF YOUNG

The Yellowstone deer arrive on summer range as soon as food plants have reached a stage of development attractive to them. This development of vegetation varies with the season and may result in the deer ascending to summer range between the middle of May and the first of July. The gray coat of winter gives way to the summer "red" early in June. Ordinarily, the young are born late in June or early in July, after the females have reached their favorite summer grounds. During this time, the does and bucks do not associate. The males tend to frequent levels slightly higher than the summer range of the does, and, as might be expected, the daily movements of the bucks take them over a wider range of territory than is covered by individual females. Hall (1927) has concluded that home range in summer covers an area of two square miles. My observations lead me to agree that bucks cover such a territory and that does with fawns are content with half that area. During many of the night and early morning hours, the animals are engaged in feeding. At midday and until late afternoon, they habitually recline in chosen spots, "beds," where they may chew cuds and relax. Usually, these resting places are selected with an eye for cover. They are often so situated that the approach of possible enemies may be from but one side, and that side is under constant surveillance by the reclining animal. It is not unusual for two or more animals to bed down near each other, in which case it is to be inferred that they divide their watchfulness in such a way as to command views of all avenues of approach to their bower. Caring for young, securing food from an abundance of forage plants, resting, and evading enemies make up the daily program of a mule deer on summer range.

FOOD HABITS

Most significant of summer activities from the standpoint of the problem with which this paper is chiefly concerned are the feeding habits. Deer are equipped with sharp lower incisors, which close upon the toothless tip of the upper jaw. Tough twigs and succulent herbs alike are cut by this mechanism. The biting off of forage involves a forward and upward movement of the head and allows close grazing or digging out of root systems, some of which are regularly sought by the animals. Buds, flowers, seeds, leaves, and twigs all come within the deer's bill of fare. The tongue is especially adapted for manipulating morsels of any variety, excluding from the mouth any unpalatable matter which inadvertently enters with food. However, the delicate nose and mouth of the deer permit of a precision of browsing and grazing

which makes for skillful selection of food. Feeding takes place rapidly, and there is but little chewing of vegetation before it enters the paunch. When this first stomach is filled, the deer retires to a place where it may recline in safety and there it chews its cud until the food is well masticated and passed on to the omasum and the true glandular stomach.

Food plants taken by deer on the Yellowstone summer range are of wide variety. Those listed have, for the most part, been observed by the writer to be actually fed upon. Rangers, ranger-naturalists, and Forest Service officials have added to the list. The list in its entirety would, perhaps, not be necessary for the purposes of this paper, but since little or nothing on food habits of Yellowstone deer has been made available, it seems desirable to present all results of the present study. Rydberg (1900) and Conard (1928) have been referred to for usage of names.

The following plants are commonly eaten by Yellowstone deer on their summer range: *Ceanothus velutinus*, redroot, "mountain mahogany"; *Chenopodium album*, pigweed; *Cornus instolonea*, red osier dogwood; Fungi—many species of mushrooms; *Lepargyrea canadensis*, Canadian buffalo-berry; *Polygonum amphibium*, false bistort, knot grass; *Populus tremuloides*, aspen; *Rubus strigosus*, red raspberry; *Salix pseudomonticola*, *S. pseudo-myrsinites*, and *S. wolfii idahoensis*, willows; *Sambucus melanocarpa*, elderberry; *Saxifraga saximontana*, saxifrage; *Sorbus scopulina*, mountain ash; *Taraxacum officinale*, dandelion; and *Trifolium rydbergii*, clover.

The following plants are apparently of intermediate importance: *Agropyron tenerum*, wheat grass; *Artemisia tridentata*, sage; *Aster adscendens*, *A. fremontii*, and *A. integrifolius*, asters; *Astragalus alpinus*, vetch; *Berberis repens*, Oregon grape; *Bromus porteri*, brome grass; *Calamagrostis canadensis*, grass; *Carex festivella*, *C. raynoldsii*, and *C. rostrata*, sedges; *Chamaenerion augustifolium*, fireweed; *Chrysothamnus lanceolatus*, rabbit brush; *Cogswellia platycarpa*, wild parsnip; *Delphinium glaucescens*, larkspur; *Festuca idahoensis*, fescue grass; *Fritillaria atropurpurea*, spotted lily; *Geranium viscosissimum*, red geranium; *Juncodes parviflorum*, woodrush; *Koeleria cristata*, June grass; *Lupinus parviflorus*, lupine; *Melica spectabilis*, melic grass; *Phleum alpinum*, timothy; *Poaepilis* and *P. pratensis*, blue grasses; *Potentilla fruticosa*, cinquefoil; *Ranunculus purshii* and *R. reptans*, buttercups; *Rhus trilobata*, sumac; *Ribes hudsonianum* and *R. parvulum*, currants; *Stipa richardsoni*, stipa grass; and *Vaccinium membranaceum*, low huckleberry.

It should be explained that this list is based on too few observations to be regarded as infallible. If a plant finds a place on the list because it was observed to be taken once, it has been grouped with others judged to be of "intermediate importance," yet further study might show that the same species is very commonly eaten, and perhaps more acceptable to the deer than some other species now listed as commonly eaten. The list is to be considered as

provisional. It finds its greatest value in that it provides a basis for comparison with winter food and offers a point of beginning for thorough investigation of the feeding habits of deer.

Summer food plants most frequently observed to be eaten are mountain mahogany (*Ceanothus velutinus*), pigweed (*Chenopodium album*), red osier dogwood (*Cornus instolonea*) mushrooms, Canadian buffalo-berry (*Lepargyrea canadensis*), aspen (*Populus tremuloides*), red raspberry (*Rubus strigosus*), willows of several species (*Salix*), elderberry (*Sambucus melanocarpa*), dandelion (*Taraxacum officinale*), and clover (*Trifolium*). During the early days of May, when deer first arrive on summer range, grasses (*Agropyron*, *Calamagrostis*, *Festuca*, *Koeleria*, *Melica*, *Poa*) are green and succulent and at this time take an important place on the animal's bill of fare. In fact, it seems to be the development of these grasses which controls the spring migration. Some few aspens, *Populus tremuloides*, not yet erect after the depressing effect of snow drifts, provide desirable browse in the form of new leaves. By the end of May, unless unusually cold weather prevails, other shrubs and forage plants (*Chenopodium*, *Lepargyrea*, *Rubus*, *Salix*, *Sambucus*, *Trifolium*) have produced an abundance of food, and normal life of the summer range is under way.

Deer on summer range are not greatly hampered by competition with other animals. Elk and moose frequent the same range, and the elk, especially, partake of many of the forage plants sought by the deer. The elk run in herds and noticeably affect the forage where they have browsed. I have noted that deer tend to avoid the areas occupied by elk in summer and that they do not feed in the immediate vicinity of regions over which elk have recently browsed. However, the deer of Yellowstone are comparatively few, and there is ample summer forage unaffected by elk.

Weights of stomach contents were recorded in three Yellowstone deer from summer range. None of the three was filled to capacity. The macerated food, a great percentage of which was not recognizable, weighed two pounds and one ounce in a male fawn about two months old, five pounds and four ounces in an adult doe, and five pounds and five ounces in a two year old buck.

FALL MIGRATION

In September, the central plateau region experiences temperatures well below freezing, and the vegetation assumes the aspect of fall. Willows and aspens turn yellow early in September, as do the plants of the open meadows. Not infrequently, snow storms occur in September. The snow of these early storms usually melts soon after falling, but at this time a restlessness develops in the deer of the upper limits (8500 feet) of summer range. Fall migration may be said to be initiated by these early storms, for a definite movement of deer from the highest levels takes place when they occur. This movement is

not the persistent descent to definite winter range which marks the true migration that later takes place from central summer range, but rather a deliberate extension of daily movements which results in travel to lower altitudes. The activity is not prompted by inaccessibility of food, for the first loose snow does not bury food plants to a depth of more than a few inches. It is, perhaps, a reaction to the warning provided by the fall in temperature, the presence of snow, and the changed condition of food. If snow storms do not occur until late October, when winter sets in earnestly and suddenly, there is a tendency for some of the deer to begin their descent in advance of snow storms. However, delayed winter conditions seem to delay fall migration.

DETAILS OF MOVEMENTS

By far the greater number of Yellowstone deer have spent the summer on ranges of intermediate altitudes (7500 feet). Here the does, fawns, and some bucks, especially the younger bucks, have congregated in small family groups, the daily movements of which have taken them over rather limited territory. In October, these have been joined, perhaps, by some of the old bucks that have spent the summer at higher levels and participated in the first "drift" of the fall. The first snow storms that affected the old bucks may also bring about some movement among the animals on the central summer range. A descent of a few of these animals often results in the appearance of deer at Mammoth and other parts of the winter range soon after the first storms of October. Animals at points distant, some fifty miles from their winter range, will at this time start a slow journey toward winter feeding grounds. This movement may not result in notable change in altitude, but it brings them within easy striking distance when the necessity for rapid descent is upon them. Such movements frequently just precede or coincide with the elk migration, and routes followed are usually parallel with the lanes of travel used by the elk. One interesting exception has been noted by Murie (1929, ms.), who finds that the deer of the Upper Yellowstone-Thorofare regions move eastward from the Yellowstone Valley, over the Absarokas to the Shoshone drainage system (Fig. 1). This is a marked departure from the usual establishment of migration routes, since a major divide between river systems is crossed. It would seem that habit forming must be responsible for the situation rather than simple environmental influences. The preliminary activity serves to stir the entire deer population, and, although by far the greater number of the animals are yet at levels more than a thousand feet above winter range, they are far from their home territory of the summer and in position to descend when forced to do so.

Severe storms usually occur in November. The restlessness, which for some weeks has been evident in the animals, culminates in a determined descent when the first severe storm arrives. The deer move in numbers to the true winter ranges and frequently seem to occupy their ancestral winter

homes overnight. If, after some days or weeks on winter range, mild weather conditions again prevail, there may be some ascent to regions immediately adjacent to, but a thousand feet above, winter range. Food plants at this altitude may differ markedly from the forage of adjacent valleys, yet they are utilized if snow conditions permit. No great distances are traveled during these untimely ascents, but the movements, nevertheless, constitute a desertion of what is ordinarily designated as winter range. With the return of severe winter conditions, the deer again move to lower levels. In other words, the deer of Yellowstone occupy that portion of their territory upon which food is available and adjacent to suitable winter range regardless of the calendar.

Coyotes and other predators prey upon the deer of Yellowstone Park (Skinner, 1927), but the extreme assertions of some of those concerned with control of predators in the park region (Henderson, 1930) (Cottrell, 1928) cannot be substantiated (Adams, 1930; Hall, 1930). Predators follow deer and other large mammals in migration, but I have found no evidence that they affect in any way the seasonal movements of deer.

INSTANCES OF ABSENCE OF MIGRATION

A significant instance of absence of migration is provided by the group of some seventy Yellowstone animals that regularly inhabit the Upper and Lower Geyser basins and the Firehole Valley between those basins and Madison Junction (Fig. 2). This area is 7500 feet above sea level, well within the summer range of the Central Plateau, and distinctly removed from other areas of winter range. No evidence of members of this group leaving their home territory has been noted by the park rangers who reside in the geyser basins throughout the year. These animals are assured of a ready food supply regardless of the severity of the winter. The heat of the geyser regions causes large tracts of land to be entirely free from snow, and the warm waters of brooklets and larger streams encourage the growth of mosses and grasses along their banks throughout the winter. These green plants provide a dependable food supply within certain limits, and it is unnecessary for the deer of the region to migrate.

WINTER RANGE AND WINTER ACTIVITIES

The area along the Gallatin, Lamar, Gardiner, and Yellowstone rivers constitutes the range to which the writer's study was given for the purposes of this paper. Other areas indicated on the accompanying map (Fig. 1) were under observation by National Park or Forest Service officials and were reported upon by them. During the period of heavy snow and low temperatures, the deer usually remain at altitudes below 7000 feet.

It is not unusual for the animals to congregate in herds in the regions in which resort is made to artificial feeding. Fifty-five is the maximum number I have observed in one herd at the game ranch below Gardiner. Park rangers

report herds of seventy as not unusual. Small bands of six to twelve are commonly encountered in all areas occupied as winter range. Late in the winter, bucks tend to separate from the bands of does and yearlings to forage alone or with one or two companions of their sex. In the region about the game ranch, they do not hesitate to join the herds of does and fawns about the hay at the time of feeding.

BREEDING

During the last weeks that the animals are on summer range, the fall molt takes place. Shedding may begin late in August and continue until the last of September. When the movement to winter range occurs, the animals are almost without exception in the full gray coat of winter. Antlers which have carried velvet all through the summer are polished, hard, and white early in September. This condition is attained some weeks before the fall drift starts and nearly two months before the breeding season begins.

Early in November and before the majority of deer have reached winter range, the rut begins. It is first evident among animals at 6500 feet or lower, and as the migration gets under way, it quickly develops to its height and continues well into December. In 1929, breeding began in October, which is unusually early. Normally, there is some breeding activity while the animals are enroute to winter range, but since most deer reach winter range before showing signs of the sex urge, I believe no necessary correlation between the two activities can be established. Table I shows the dates of breeding in the Yosemite region over a period of six years. Records for the Yellowstone region are inadequate for the preparation of such a table.

Evidences of the rut are unmistakable to one familiar with deer behavior. The bucks manifest a restlessness and a tendency to assume a pose which is strictly characteristic. In the presence of does, a breeding buck will repeatedly lower his head so as to lay his antlers back near his shoulders and stretch his neck to the utmost. The base of the skull is depressed, the tip of the nose elevated, and the nostrils distended. This posture of the head and neck is often maintained when trotting in pursuit of a doe as well as when standing. Not infrequently during the rut, bucks give voice to a low, deep-pitched *b-a-a-a*. This sound is especially apt to be uttered when the animal is maneuvering with a doe, impatient with a bothersome fawn or angered with a rival buck.

When intent upon a doe at rutting time, a buck is commonly quite oblivious to other affairs among animals or to human beings that may be near. It is evident that the sensitive nose of a sexually active buck can pick up the scent of a doe in heat, although this female may have passed from his locality some minutes before. Bucks habitually follow the trail of rutting does and, like a dog, with nose to the ground trace the tracks of the desired animal through

a maze of trails made by other deer. I have observed such pursuit to culminate in success for the buck after twenty minutes of blind trailing by scent through a half mile of fairly dense brush cover.

It would appear that does make no particular attempt to separate from their fawns during the rut. The incessant chasing to which they are subjected at this time results in great disturbance to their usually quiet daily routine, and instances have come to my notice of fawns being lost temporarily. In some cases, such separation occurred in families readily identified, and it was noted that a reunion of fawns and mother took place when the female no longer excited the attention of bucks. As a rule, however, the fawns race along with the beset mothers, and quiet family affairs are resumed after the rut. It is not until a short time before birth of fawns that the doe rids herself of the company of her young of the preceding year. Bucks intent upon serving a doe may become impatient with her ever-present fawns, and it is not unusual for them to make half-hearted lunges at the troublesome youngsters, but I have known of no truly purposeful attacks upon the offspring of a mate.

Conflicts between bucks are the exception rather than the rule. During the period of the hardening of the antlers, before the beginning of the rut, friendly wrestling matches between bucks are numerous. The contestants deliberately lock antlers and engage in rather strenuous bouts which may last, with intermittent breathing spells, for an hour. But when the period of actual breeding arrives, there is an evident careful hesitancy to engage in combat. Large bucks intent upon serving a doe encounter small opposition from other bucks. Small bucks in pursuit of a female yield to larger animals if their claim is disputed. I have witnessed but one true fight between breeding bucks among the thousands that have been under my observation. On this occasion, December 12, 1927, two eight-point bucks encountered each other near the foot of Yosemite Falls. No doe was in the immediate vicinity. The battle consisted of a series of terrific clashes launched when the animals were a few feet apart and interspersed with exhausting wrestling with antlers locked. One animal consistently gave ground to the other and at the end of five minutes turned tail and ran. But two other actual combats have been reported in Yellowstone or Yosemite during the eight year period that this study has been in progress (Michael, 1926).

Observations of actual coition are not as numerous as might be expected. But four instances of reports from eye witnesses were brought to the Yosemite Museum during my years there, and I failed to find a Yellowstone resident who had been witness to the act. It was not until the fall of 1930 that I was enabled to observe a buck cover a doe. The following notes are extracted from my Yellowstone field notebook:

"Nov. 14, 1930. This afternoon in driving to Gardiner I noted a number of deer in a state of agitation because of the activities of two amorous bucks.

They were but one hundred yards from the road, in open sagebrush country and nicely delineated against the eight-inch cover of new snow. I determined to secure pictures and rather deliberately set up the $6\frac{1}{2}'' \times 8\frac{1}{2}''$ view camera equipment. There were seven deer in the group. One fine eight-point buck devoted himself to a doe with a single fawn. A smaller buck was much interested in a doe followed by two fawns. The two groups, constantly moving because of the short rushes of the bucks, were some fifty yards removed from one another. Because of close proximity and absence of interfering vegetation, I selected the eight-point buck and his doe as subjects for the picture. The buck obliged by constantly assuming the pose so characteristic of the rut and made frequent rushes for the doe. She would evade him, as has always been the case with such does I have watched, and after a run of fifty yards or so return to the near vicinity of the station occupied when I began my observations. Occasionally, her trot would drop to a walk, which would permit the buck to nose about her tail. Her fawn of the year followed her constantly and was occasionally a hindrance to the buck, whereupon he would make half-hearted efforts to hook the young one with his antlers.

"I had watched this performance for about ten minutes, made two exposures, and put the camera in readiness for a third, when the doe, evading one of the sudden rushes of the buck, ran about thirty feet from him, with obvious kicking of heels and shaking of head not noticed in her previous escapes, and came to a sudden stop. She stood with her tail toward the buck and in evident expectation. He trotted up to her, head down, and without hesitation covered her. He remained upon her not more than four seconds, I think. I snapped a picture while he had her covered. The pair stood exactly broadside to me. I noticed no particular muscular movements of either animal during the act. The doe stood perfectly still. In fact, her attitude from the moment she stopped was that she anticipated the events that transpired. I believe the buck got off without her moving. Afterward, they remained near each other. The doe frequently lifted her tail in a manner not typical of the animal at other times, and a marked spasmodic contraction of the external genitalia was evident. The buck continued to follow when she moved short distances. The doe smelled about his nose, his antlers, and his tail in a caressing manner. There was no further intercourse during the additional fifteen minutes that I kept the pair under observation."

By the close of the rut in December or January, the bucks present a worn appearance, characterized by loss of flesh, dejected postures, and apparent stiffness of joints. A few weeks after the breeding period closes, antlers are dropped, and both males and females enter upon a period of quiet living upon the winter range.

FOOD HABITS

The following observations are based on notes taken in the Lamar-Yellowstone section. The variety of food available on winter range is much limited as compared with the numerous species of plants fed upon in summer. The most favorable areas of winter range experience minimum temperatures of -30° F., with mean temperatures of 0° not at all uncommon. Snow

on winter range is not excessive, five to fifteen inches being usual. High, persistent winds cause the snow to drift, so that numerous exposed slopes and elevations are swept quite clean. The deer seek out sheltered timbered coves in which to rest and at feeding time venture into deep snow to take advantage of sagging limbs of trees that have inclined under the weight of snow, or go out to exposed areas from which the snow has been blown away. Wm. Rush (1930) advances the idea that it is the condition of the crust of snow which determines distribution of elk, rather than the depth of snow. If snow is loose, he finds that elk remain at high altitudes in spite of low temperatures and deep snow. It has been my observation that the deer of Yellowstone do not so frequently paw through the snow for food as do the Yosemite animals, or as do the elk of Yellowstone.

COMPETITION WITH OTHER LARGE ANIMALS

In winter, Yellowstone deer come into direct competition with three browsing and grazing animals: mountain sheep, antelope, and elk. Buffalo constitute a fourth competitor in parts of the winter range. The same food plants sought by deer are hungrily consumed by the others (Bailey, 1930; Skinner, 1928). In primitive times, the animals of the park area descended to regions far removed from the present winter range and secured their food from areas of wide extent and ample capacity. Present day conditions of human occupancy of the old winter haunts prohibit such spreading. A fence through the present winter range and along the north boundary of the park tends to discourage the extended drift of the animals and, except in instances of very severe winters, serves to keep them within the bounds of national park protection. Recent investigations (Rush, 1931) indicate that food of the present winter range is not less nutritious than was the forage on the primitive range.

The congestion which results from the enforced limitation of drift over-taxes the natural capacity of the range and makes necessary the artificial feeding with hay. All of the large mammals participate in the benefits of such feeding and all of them have changed their normal habits accordingly. It is evident, however, that the supplementary feeding of hay has not greatly affected the natural feeding upon native plants, for this section of the park is consistently grazed and browsed upon to the point of near ruin. Plants observed to be fed upon in winter are: *Amelanchier alnifolia*, June berry; *Artemisia* (several species), sage brush; *Chrysothamnus lanceolatus*, rabbit brush; *Festuca* sp., fescue; *Juniperus scopulorum*, Rocky Mountain cedar; *Juniperus sibirica*, ground juniper; *Pinus flexilis*, limber pine; *Poa* sp., blue grass; *Populus tremuloides*, quaking aspen; *Prunus melanocarpa*, choke cherry; *Ribes cereum*, squaw currant; *Ribes viscosissimum*, sticky currant;

Rosa acicularis, wild rose; *Ribes setosum*, wild gooseberry; *Salix fluviatilis* and *S. pseudomyrsinites*, willows; *Stipa* sp., spear grass; and *Symphoricarpus occidentalis*, snow berry.

SPRING MIGRATION

For about five months the Yellowstone deer must contend with winter conditions of a severity not approached in the Yosemite region. These conditions are moderated in March, when mean temperatures steadily climb. In the vicinity of Mammoth Hot Springs, snow disappears in March or April. Exact dates of disappearance of snow during the three years that this study was in progress are 1928—April 10; 1929—March 27; 1930—April 2. The snow line rapidly retreats and by early May is usually near the 8000 foot contour line. It might be expected that deer would follow the ever-climbing snow line and so arrive on summer range at about the time that the Central Plateau was free from snow. This is not the case.

The advent of mild temperatures at the 6200 foot level during April brings about rapid development of new grasses. By April 15, an abundance of green forage is available on winter range. Important among these plants are: *Bromus* sp., brome grass; *Calamagrostis canadensis*, reed grass; *Festuca idahoensis*, fescue; *Panicularia nervata*, manna grass; *Poa pratensis*, blue grass; *Stipa richardsoni*, spear grass; and *Taraxacum ceratophorum*, dandelion.

This succulent herbage holds the deer to the scene of their winter difficulties until similar growth of new vegetation takes place at higher levels. Bucks tend to lead the way to new feeding grounds. The upward drift begins with a very gradual extension of daily movements and results in a scattering of the animals that during the winter had congregated in sections of the winter range. For more than a month after the disappearance of snow, however, deer remain at levels designated as winter range. A few elect to remain all summer. The true upward movement is coincident with the development of green vegetation at higher levels, and arrival on summer range does not occur for some twenty days after snow has melted from the 7500 foot level. These individuals that travel to the upper limits of summer range appear to climb very slowly from the 7500 foot level and do not appear at 8500 foot elevations for about a month after most of the snow has disappeared from these high elevations. By this time, the middle of June or later, spring has arrived on the heights. It is very evidently availability of food that regulates the spring migration in the Yellowstone country.

The condition of forage plants also affects the routes of travel. As an example of the influence of spring growth upon the path of migration, circumstances attending the movement of about 300 deer of the Mammoth-Gardiner-Mount Evarts winter range may be described. Two natural exits

exist which might be expected to serve as lanes of travel from the depressed basin in winter range. One route, via Snow Pass to the park plateau at Swan Lake, leads westward and necessitates a climb of 1500 feet in four miles. The other route, via Lava Creek and Crescent Hill, leads eastward (Mammoth-Tower Falls Road) and requires about fifteen miles of travel with the same ascent (1500 feet). Investigation shows that the longer route comes into use a week earlier than does the other and that a far greater number of animals, both elk and deer, follow the eastward route. In the spring of 1930, new growth of grasses and leaves of shrubs were noted to be well advanced in the vicinity of Crescent Hill (7500 ft.) on May 4. Examination of forage plants in Snow Pass (7400 ft.) on the same date showed that a moss in small streamlets was the only representative of green vegetation. The entire route from Mammoth to Crescent Hill afforded an abundance of new growth, while no spring growth was in evidence eight hundred feet below Snow Pass. On May 4, numerous deer were traveling toward Crescent Hill, and on May 7, a veritable migration was under way there. It was not until May 11 that the first deer went through Snow Pass. No conclusive evidence exists upon which to base the statement that deer would not first follow the Lava Creek route even though topographical conditions were such as to bring about uniform development of plants along both routes. It seems reasonable to conclude, however, that the earlier production of forage along the eastern route serves as an inducement to start a large percentage of the deer of the Mammoth region upon this longer way to summer range.

Data on the migration route of an individual Yellowstone deer have been provided by members of the park's ranger and educational staffs. In 1921, a buck, "Wheezy," demonstrated tendencies to become very friendly with members of the human population at Mammoth Hot Springs, within his winter territory. Because this animal was possessed of an unusual head, he came to be recognized by all residents. This intimate acquaintance, over a period of years, made possible significant reports on his seasonal movements. His summer range was near the Thumb on Yellowstone Lake. In leaving Mammoth in the spring, he journeyed by way of Lava Creek, Crescent Hill, Tower Falls, Dunraven Pass, and Canyon to Lake. This route is not less than fifty miles in length and probably more than sixty miles. In the fall, the same route was retraced. Unfortunately, no records were made as to time involved in making the journeys.

THE MULE DEER OF THE YOSEMITE REGION

Conditions of the Yosemite region range from the hot, dry slopes of the brushy foothills to the bleak regions of glaciers and perpetual snow on the mountain tops. The slopes are beautifully watered by springs, creeks, rivers, ponds, and lakes. Granite bosses, tremendous cliffs, glacial moraines, great

canyons, and rock-rimmed basins unite to give an irregular topography which provides southward-facing slopes bathed by long hours of sunlight and shady, moist north slopes little affected by direct sunlight. On the long gradual western slope of the Sierras, the mule deer are found in greatest abundance in summer within the beautifully timbered Canadian and Hudsonian Zones. In winter, the greater number of animals descend to the Upper Sonoran area, although some may remain in the Transition Zone, and a small percentage occupy the foothill belt, or Lower Sonoran Zone.

Sierra Nevada mule deer have received frequent casual mention in printed accounts of the region ever since Leonard's narrative of the 1833 Walker Expedition appeared in 1839, but truly significant accounts of the animal did not appear until very recent years. Grinnell and Storer (1924) have accorded the species a good general treatment, and more recently Grinnell, Dixon, and Linsdale (1930) have added a valuable account. Hall (1927) has published notes, many of which apply to the Sierra deer.

In Yosemite National Park, the mule deer constitutes one of the most interesting features of the area. It is present in surprising numbers and within the past ten years has so changed its habits as to be continually on exhibition somewhere within the park. The 1930 animal census from the park superintendent's office indicates a deer population of 16,000. I believe this number falls short of the total number of animals which inhabit the park in summer. Prior to 1925, no one would have estimated a Yosemite deer population of more than 5000. In 1924 and 1925, some 22,000 deer (actual count) were killed because of the epidemic of foot and mouth disease, which affected a part of the deer of the Sierras (Mohler, 1926). This regrettable happening at least provided authentic data upon which to base future estimates of deer numbers. Most of the slaughtered deer had resorted to the northern part of Yosemite National Park in summer. They constituted the so-called "Tuolumne Herd," and their summer range represented less than half of the available summer range within the park. There is no reason to believe that the Merced drainage system was less densely populated than was the Tuolumne. On the contrary, observations would indicate that a greater number of deer frequented the southern half of the park. During the four years that have elapsed since the Tuolumne herd was so nearly destroyed, the animals of the Merced region have greatly increased in numbers. The Tuolumne animals have "come back" slowly, and there can be no good basis of reasoning which would place the present Yosemite deer population at less than 30,000.

SUMMER RANGE AND SUMMER ACTIVITIES

An ever-growing number of Yosemite deer are responding to the influence of artificial conditions created by man and choose to remain in Yosemite

Valley (Transition Zone) the year around. Actually, this group of non-migrants represents a percentage of the total deer population that is hardly appreciable, and like a few deer that spend the entire year in the Upper Sonoran Zone, may be ignored in relation to the general applications of the present studies. Non-migrants are given further mention elsewhere in this paper. By far the greater number of deer of the Yosemite country travel to the Canadian and Hudsonian Zones (6200 feet to 10,500 feet) for the summer. The heart of this summer range lies about the 7500 foot level. Some deer, old bucks especially, frequent the bare granite ridges near timber line. During high-country studies, I have frequently come upon bucks in such situations. The greatest altitude at which I have found them is 10,000 feet on Tenaya Peak. Old bucks are not uncommonly accompanied by a younger male, and sometimes three males associate during their weeks on the heights. The highest Yosemite record (Grinnell and Storer, 1924) is 10,600 feet at Fletcher Lake.

The region of summer range is characterized by rounded prominences and shallow canyons forested with splendid stands of jeffrey pine and red fir. In certain areas the lodgepole pine, *Pinus murrayana*, predominates. Huckleberry oak and snow bush predominate in the brush cover. Quaking aspen, *Populus tremuloides*, occurs in groves of splendid trees and in dense thickets of brush and saplings. At the upper limits of summer range, jagged peaks and bare granite ridges replace the forested prominences. Just below these heights occurs the boreal forest of mountain white pine, *Pinus monticola*; white-bark pine, *Pinus albicaulis*; and alpine hemlock, *Tsuga mertensiana*. Willows, *Salix glauca villosa* and others; Sierra maple, *Acer glabrum*; dwarf manzanita, *Arctostaphylos nevadensis*; wormwood, *Artemisia norvegica*; and Labrador tea, *Ledum glandulosum* represent the shrubs of the ground cover.

REARING OF YOUNG

On the summer range, few enemies harass the deer, and the summer activities comprise carefree daily movements in an abundance of browse with successful family affairs, which nearly always result in each doe escorting two well grown fawns to winter range. The young are born in June or early in July, soon after the mothers arrive on summer range. In 1924, I found a new born fawn on June 15. T. J. Jones of the Inyo Forest, in his annual report of 1925, states that the first fawn observed by him that year was born June 20. G. S. Way of the Inyo Forest saw the first fawn of 1929 on June 4, and this constitutes the earliest record of the Yosemite region. Usual dates of arrival are later, as indicated in the following table, which is based upon my observation unless otherwise indicated and is included here in order to throw light on the period of gestation:

TABLE I. *Breeding Dates and Arrival of Young for the Yosemite Region.*

Years	First noted evidence of rut	Last noted evidence	First noted fawn	Last noted fawn
1923-24	Nov. 12	Dec. 31	June 15	July 17
1924-25	Dec. 12	Jan. 10	June 20 ²	June 26
1925-26	Dec. 10	Jan. 21	June 26	July 15
1926-27	Dec. 16	Jan. 25	June 21	July 15
1927-28	Dec. 1	Jan. 14	June 29	July 9 ¹
1928-29	Nov. 26	Feb. 20 ¹	June 4 ³	
1929	Nov. 28			

¹Reported by George M. Wright. ²Reported by T. J. Jones ³Reported by G. S. Way.

Most of these observations on birth of young were made among deer that did not migrate but spent the summer in Yosemite Valley. The family cares of such animals are not so effectively concealed from the thousands of human beings who swarm over the area, and reports of tiny fawns are repeatedly brought to the Yosemite Museum or to the Chief Ranger's office. One of the trials of the ranger department during the period of fawning is the prevention of thoughtless "kidnapping" of very young fawns by tourists, who find the cached infants near their camping sites and are at once moved to "save" the "helpless little thing" that has been "deserted" by its mother.

On June 21, 1927, I obtained my only opportunity to record observations on a newly arrived fawn within the true summer range, where the great majority of fawns are born, but where incidents relating to their early care are seldom observed because of the precautions of the mothers, the vastness of the territory, and the sparseness of the human population. I had arrived at Merced Lake (7200 ft.) and about sundown was investigating possible inhabitants of willow thickets adjacent to a remarkable open forest of aspen, which exists at the upper end of the lake. I walked noiselessly between the trees, avoiding the few bushes and taking advantage of the spongy humus which covered the ground. As I gained a position which enabled me to look into an embayment in the thickly-growing willows, I was accorded a splendid view, at a distance of forty yards, of a doe engaged in licking the coat of a very young fawn. The little animal's long legs were wobbly but strong enough to indicate that it was at least twenty-four hours old. Apparently, it had just nursed. I made no effort to approach closer but was not long unobserved by the mother, who caught my scent or noted some small movement and bounded noiselessly out of sight behind the willows. The fawn made one awkward leap and flopped to the ground as though shot. The leap had sufficed to bring its body under the cover of over-hanging leafless wil-

low stems, and its spotted brown coat caused it to be nearly invisible in the failing light. I walked up to it, and it made no move. Its eyes remained open, and there was no movement of eyelids. I touched it with my fingers, and it responded with but the slightest wince of hip muscles I had touched. I made no further effort to disturb it. Other very young fawns which I examined in Yosemite Valley (six in all) reacted to my investigations in much the same manner. The characteristic "freezing," together with protective coloration and evident absence of scent (usually even the metatarsal gland of a very young fawn has no odor) no doubt save many fawns from preying beasts that would otherwise make meals of them.

I attempted to locate a possible twin of the Merced Lake fawn but did not succeed. I saw no more of the mother. The next morning, soon after daylight, I looked for the fawn and its mother but found neither of them. It is rather surprising that the thousands of small fawns which are born in the Yosemite high country do not more frequently come under the observation of the park visitors who walk through their haunts, but the fact that they are seldom noted is good evidence that the does of the high country have not relaxed in their habits of caution as have the semi-domesticated animals that spend their lives among the human habitations in Yosemite Valley.

A female fawn a few hours old on June 30, 1927 weighed six pounds and two ounces. On July 10, 1928, Wright and Dixon weighed two fawns known to be twenty-four hours old. The female weighed six pounds, four ounces; and the male, six pounds, ten ounces. On August 9, 1930, a Yellowstone fawn, about two months old, was found to weigh forty pounds (dead weight). A Yosemite fawn, about four months old, was killed October 26, 1929 by jumping into a snag which penetrated its lungs. It weighed fifty-nine pounds and two ounces. Its stomach contained material weighing four and one-fourth pounds.

Yellowstone rangers have reported that fawns take forage plants in their second week. Hall (1927) states that deer of the Kaibab Forest Reserve take forage at the age of two weeks. I have been unable to observe Yosemite fawns taking plant food at this age. For about one month, Yosemite fawns do not follow their mothers in the day time. Tiny tracks in the sands of lake shores and stream banks indicate that very young fawns accompany the mothers to drinking places at night, and it is probable that they move about with the does rather freely under the cover of darkness. In Yosemite Valley, where semi-domestication has resulted in a change of habits and lessening of vigilance, fawns quite commonly follow the mothers when six days old. I have watched these active youngsters carefully in an attempt to discover at what age they take plant food. I have seen no fawns that I could judge to be younger than one month attempt to browse or graze. Those that have been watched when making their first attempts to take such food have

always evidenced an awkwardness and doubt which suggest no avid appetite.

During the period of early development, fawns have little strength. As has been stated, they remain in concealment during hours of daylight and are probably more active at night than is generally supposed. Summing up personal observations made over a five-year period in Yosemite, I conclude that the mothers frequent the immediate neighborhood in which the young are hidden and come to the cached infants twice during hours of daylight to permit them to nurse. These visits occur anytime during a two hour period before midday and again during the late hours of afternoon. The does apparently make no attempt to keep in sight of the fawns' hiding places. Fawns more than a week old are with the mothers during many hours of the night and perhaps nurse more frequently than in the daytime. After attaining an age of five weeks, the fawns begin to take a considerable quantity of forage, but continue to nurse until the last of September. After this time, the does are reluctant to nurse them, but fawns frequently show a rough insistence upon mouthing the mother's teats even during the breeding season in late November.

In Yosemite, the spotted coat of the fawn begins to disappear in August and by the close of September has been replaced by a gray coat, which is often characterized by an abundance of long silky hairs not evident in older animals.

FOOD HABITS

The west slope of the Sierra Nevada, so much of which is occupied by deer, is abundantly watered and produces a great variety of flowering plants. No less than 1200 species and subspecies occur in the Yosemite region, and among these the deer find a wide variety of forage. On summer range, fifty per cent of the food taken comes from a half dozen species, but about forty others are very commonly eaten, and the complete list of plants known to be fed upon includes about one hundred species. Continued study would, no doubt, add many others to the list. Buds, twigs, soft fruits, and seeds and roots, as well as leaves, find places in the deer's diet.

Following is a list of all species of plants known to be fed upon in summer. The list is divided into two groups: those known to be commonly eaten, and those thought to be less frequently partaken of. It is based upon my personal observation, the reports of Yosemite ranger-naturalists, the notes of Dr. H. C. Bryant (Hall, 1927), and J. Dixon's (1928) published records. Names are based on the usage of Jepson (1925).

The following plants are commonly eaten: *Amelanchier alnifolia*, western service berry; *Arctostaphylos nevadensis*, dwarf manzanita; *A. patula*, green manzanita; *Calochortus nudus*, Sierra star tulip; *C. nuttallii*, Mariposa lily; *Ceanothus cordulatus*, snow brush; *C. integerrimus*, deer brush; *C. prostratus*, mahala mat; *Chenopodium album*, white pigweed (lower limits of

summer range; introduced); *Cornus pubescens*, creek dogwood; *Erigeron coulteri* and *E. ursinus*, flebanes; *Festuca elatior*, meadow fescue (European); *F. supina*, fescue; fungi, various species; *Helenium bigelovii*, Bigelow sneezeweed; *Lotus oblongifolius*, hosackia; *L. torreyi*, meadow hosackia; *Lupinus breweri* and *L. lyallii*, lupines; *Notholcus lanatus*, velvet grass (European); *Populus tremuloides*, aspen; *Polygonum alpinus*, knotweed; *P. aviculare*, wire grass (lower limits of summer range; European); *P. imbricatum* and *P. minimum*, knotweeds; *Prunus emarginata*, bitter cherry; *Quercus kelloggii*, California black oak; *Rubus parviflorus*, thimble berry; *Rumex crispus*, curly dock (European); *R. paucifolius*, dock; *Salix glauca* and *S. jepsoni*, willows; *S. petrophila*, alpine willow; *S. phylicifolia*, var. *monica*, Mono willow; *S. scouleriana*, Nuttall willow; *S. sitchensis*, var. *coulteri*, velvet willow; *Saxifraga integrifolia* and *S. punctata*, saxifrages; *Sorbus sitchensis*, western mountain ash; *Taraxacum* sp., dandelion; *Trifolium breweri*, forest clover; *T. longipes*, clover; and *T. monanthum*, carpet clover.

The following plants are known to be eaten occasionally: *Achillea millefolium*, common yarrow; *Agropyron* sp., wheat grass; *Agrostis* sp., bent grass; *Antennaria rosea*; *Aster yosemitanus*, Yosemite aster; *Calamagrostis* sp., reed grass; *Carex* sp., sedge; *Castanea sempervirens*, bush chinquagin; *Chrysothamnus bloomeri*, rabbit brush; *Cirsium acaulescens*, thistle; *Eriogonum nudum* and *E.* sp., fleabanes; *Festuca* sp., fescue grass; *Fragaria virginiana platypetala*, wild strawberry; *Geranium incisum* and *G. richardsonii*, geraniums; *Hieracium albiflorum*, hawkweed; *Juniperus occidentalis*, Sierra juniper; *Lupinus covillei*, lupine; *Phleum alpinum*, timothy; *Poa* sp., blue grass; *Potentilla fruticosa*, shrubby cinquefoil; *Quercus vaccinifolia*, huckleberry oak; *Ranunculus alismaefolius*, butter cup; *Ribes cereum* and *R. montigenum*, currants; *R. nevadense*, Sierran currant; *R. viscosissimum*, currant; *Sambucus racemosa*, red elderberry; *Sarcodes sanguinea*, snow plant; and *Symphoricarpos creophilus*, snowberry.

Observations indicate that the following of the plants just listed are most eagerly eaten in the densely populated section of summer range (6500 ft. to 8000 ft.): *Arctostaphylos patula*, *Ceanothus cordulatus*, *Ceanothus integririmus*, *Cornus pubescens*, *Helenium bigelovii*, *Lotus torreyi*, *Populus tremuloides*, *Prunus emarginata*, *Rumex paucifolius*, and *Salix*.

Late in September and throughout October, the Canadian Zone (6200 ft. to 8500 ft.) experiences consistent frosty nights, which bring about changes in vegetation typical of fall. *Salix*, *Cornus*, *Quercus*, *Rubus*, *Ribes*, *Sambucus*, and *Castanea* are the first to turn color. *Ceanothus cordulatus* persists in its green color in spite of the lengthy period of frost, and deer continue to depend upon it for a major part of their forage. They do, however, partake of brown leaves of many species of their usual food plants and may be observed to feed on fallen leaves, as well as those that adhere to bushes and trees. Grasses at this time exist as green blades deep within the matted

dead tussocks which cover the meadows and swales, but there seems to be little attempt made by deer to secure green grass. A surprising tendency prevails to feed upon woody parts of such shrubs as *Salix*, *Manzanita*, *Ribes*, and *Prunus*.

The stomach of a fawn about four months old, killed near Bridal Veil Creek at an altitude of 7000 ft., October 26, 1929, was found to contain food weighing four pounds, four ounces. A rough classification of the contents gave the following proportions:

Finely macerated material, leaves, etc. not recognizable.....	73%
Coarse wood material, bark, stems, roots, species not recognized	22%
Remainder	5%
<i>Hieraceum albiflorum</i> , hawkweed, leaves.....	trace
<i>Ceanothus cordulatus</i> , snowbush, leaves.....	"
<i>Arctostaphylos patula</i> , green manzanita, leaves.....	"
<i>Salix</i> sp., willow, green leaves.....	"
<i>Salix</i> sp., willow, dry brown leaves.....	"
<i>Ribes viscosissimum</i> , currant, leaves.....	"
<i>Evernia vulpina</i> , staghorn lichen.....	"

FALL MIGRATION

During September and October, the summer coat of "red" is shed and replaced by the winter "blue." The molt of bucks tends to precede the change in does. By the middle of October, fawns of the year usually have produced their first winter coat, and summer spots are no longer to be seen. Some deer move to winter range while still in summer pelage, but a greater number undergo the molt while on summer range.

Records kept over a four year period reveal that the downward drift from the central summer range (7500 ft.) may start in advance of snow fall but that a part of the deer population usually remains at this level after precipitation of several inches of snow occurs and deserts these localities only after severe snow storms which quite cover food plants. Dates of the beginning of the fall drift (7500 ft. or thereabouts) range from October 10 (1928) to November 5 (1929). In nearly all instances, the downward movement from the central summer range is initiated by a snow storm. It is usual, however, for the drift of those animals that have summered at upper limits to begin without the stimulation provided by snow fall, and similar movements in advance of storms may occur among animals of lower levels. In 1929, many of the deer at Glacier Point (7200 ft.) and similar localities within the central summer range began their fall migration about October 25, more than a month in advance of the first snow storm. On that occasion, a part of the deer population slowly descended a thousand feet toward winter range. Snow storms of December 10 resulted in a precipitous rush to lower levels. For

purposes of comparison, this irregular instance is not a serious handicap in drawing conclusions, for hundreds of deer about the Glacier Point region remained on the central summer range as usual and delayed their descent until the coming of the snow storm of December 10.

Unless the early snow storms are of a severe nature, covering all zones to the normal lower limits of the snow line just below 4000 feet, the fall drift is not an impulsive rout. The first storms of the season usually result in a few inches of snow cover above 7000 feet, with greatest depth of snow at the higher levels of summer range. Any deer which may then be at 8000 feet or higher will start their migration to more favorable localities. Their descent through the belt of deepest snow will be steady and persistent. On the Glacier Point Road, during such a movement, I observed an identifiable buck travel in one hour a distance the shortest route of which would have involved five miles of travel. When a level has been reached, which permits of feeding without the encumbrance of snow, the march is delayed. If the browse of the locality is inviting, the animals will linger, and the feeding movements may result in little or no descent. If a period of warm weather follows the snow storm and the snow line is caused to retreat, the animals will in some instances ascend to slightly higher levels. No case has come to my notice in which Yosemite deer climbed more than 500 feet while en-route to winter range. It appears that the instances of animals making ascents while the fall migration is in progress result from daily feeding movements. If forage is more desirable on slopes some few hundred feet above, a movement results which takes the animal to that feeding area. The fact that upward movements, involving any great change in altitude, are exceptional during migration indicates that they are not brought about by a desire to maintain altitude merely, nor an urge to remain in proximity to the snow line. It is the presence of available food which controls the daily movements of migrating individuals just as it is the availability of food which regulates the mass movements of the deer herds of a region.

DETAILS OF MOVEMENTS

The following entry in my Yosemite field notebook is pertinent here:

"November 22, 1929. Visited the area above Chinquapin traversed by the Glacier Point Road. In the Indian Creek drainage basin, at an altitude of slightly more than 7000 feet, I found several dozen deer—does, fawns, and bucks. Some of the animals showed unmistakable evidence of intimate acquaintance with man; others were extremely shy. It is reasonable to believe that the approachable individuals had traveled from the vicinity of camp sites on the Glacier Point Road, some miles distant, and that the wary animals had descended from regions unfrequented by tourists about the headwaters of Bridal Veil Creek.

"The slopes about Indian Creek, which on October 15 were not densely populated with deer, were literally cut up like a barn yard. The animals seen

today were a part of the great "drift" that is making, or has already made its way to winter range. I remained in one neighborhood for four hours. The unhurried movements of all deer involved in the migration further substantiate the idea that the animals move down from summer range very leisurely if they are not hurried by storms. Feeding progressed in a normal manner, and with the exception of one doe, followed by two fawns, who stepped along with an apparent intention of making definite progress to lower levels, there was nothing about the movements of the animals to indicate that they were enroute to winter range. Yet a study of the maze of new trails through the *Ceanothus* indicated that very few tracks pointed uphill. The movements of individuals, deliberate though they be, result in a definite descent through a period of some hours. I found that scores of trails on the slopes picked their way along the auto road, which here passes through the canyon. Eight major trails, roughly parallel, were readily recognized (See Fig. 2). The general condition of the terrain suggests the passage of a thousand sheep, and it is evident that this shallow canyon provides a favorite route of descent from the high meadows and basins of the southern end of the park."

A special effort was made to determine relationships of food of summer months to the food taken while enroute to and after reaching the winter habitats. During a typical but decidedly active period of migration in 1929, I devoted three days, Nov. 21, 22, and 23, to studying the feeding habits of migrating deer along routes that were readily accessible from the Glacier Point Road. Data on summer food had been accumulated, as already described in this paper. Studies of winter food had been made over a period of five years and are described in succeeding sections of this paper. After considering details of feeding habits during the drift, I prepared the following summary as a record in my note book:

"Each day of the study I observed fifty or more deer enroute to winter range. Ninety-two per cent of the animals seen to feed took leaves and twigs of *Ceanothus cordulatus*. Eighty per cent of all animals sought the vicinity of, or entered thickets of *Ceanothus cordulatus*. They were either feeding or moving very slowly. The remaining twenty per cent frequented small open meadows, moved slowly without apparent purpose beneath the firs, or descended the more abrupt slopes of canyon walls. *Ceanothus cordulatus* in this section is one of the most prominent species of the chaparral and is nearly continuous from the 8000 foot level to 6000 feet. Just above the Chinquapin Station, it is replaced, imperceptibly, by *Ceanothus integerrimus*, *C. parvifolius*, and *C. prostratus*. On the south facing slopes, immediately below Chinquapin Station, conditions are such as to provide good winter deer range at 5000 feet to 5500 feet. Here *Ceanothus integerrimus* and *C. parvifolius* prevail. Along this migration route (Bridal Veil Meadows—Perego Meadows—Indian Canyon—Chinquapin), food plant conditions are quite uniform from the 8000 foot to 6000 foot levels. Within this belt the deer have slowly descended until many of them now (November 23) are at its lower margin; yet, it has not been necessary for them to change their diet greatly. The localities in which they are present in greatest numbers are im-

mediately above especially favorable areas to which they may descend in an hour should storms make such descent necessary or desirable."

For two weeks after these studies were made, I watched or had someone watch the deer of the section in question. On December 10, three inches of snow fell in regions above 6500 feet. Indian Canyon fairly spewed deer. Three days later, no deer were to be found about Bridal Veil and Peregoy Meadows, and but one young buck could be noted in the canyon of Indian Creek. In the logged-off basins below Chinquapin and just outside of the park (5000 feet), the animals flocked like sheep.

INSTANCES OF ABSENCE OF SEASONAL MIGRATIONS

It is common knowledge that the entire mule deer population of some regions habitually occupies a common winter and summer range (Seton, 1927). Grinnell and Storer (1924) point to the fact that some animals of the Yosemite region spend their entire existence in the Upper Sonoran chaparral belt. They express the belief that fawns born at low altitudes remain there throughout their lives, while those born in the mountains migrate with the change of seasons, thus implying that the habit of migrating is transmitted to successive generations through the teaching by mothers of experience. In the present paper, attention has been called to the non-migration of a part of the Yosemite deer (p. 19).

The numbers of deer occupying the areas in question are bound to be controlled by the food available. When numbers in any locality tend to become larger than the supply of forage will support, competition results in extension of daily movements of enough of the animals to relieve the pressure. In such areas as the chaparral belt west of Yosemite National Park, such extension of range is easily accomplished in either summer or winter. The idea at once suggests itself that in this competition there is the basic explanation of the origin of the migratory habit (Adams, 1919).

WINTER RANGE AND WINTER ACTIVITIES

Areas west of the summit of the Sierras to which park deer resort in winter vary in altitude according to exposure. These California animals are not forced to contend with severe winter conditions as are the Yellowstone deer and they take full advantage of their opportunities to secure favorable winter abodes. Prominences which slope south and east may, during most of the winter, afford ideal conditions at altitudes of 5000 feet or slightly higher. Such conditions prevail in the Merced Canyon above El Portal and in many places upon the slopes of the basin drained by the South Fork of the Merced and its tributaries. After snow accumulates to the great depths that are usual in February and March, there are few areas above 4000 feet in which the deer find conditions suited to their winter existence. They then descend to regions

about the snow line, which, for the purposes of this paper, has been defined as 3000 feet. The deer of Yosemite Valley constitute exceptions in this movement. When the writer's studies were begun in 1923, very few animals remained in Yosemite Valley in winter. During the years of my residence there, I was enabled to observe a marked change in habits among the animals that frequented the Merced Canyon and wintered below Yosemite Valley. The number of deer that inhabits the Valley, both summer and winter, has increased noticeably each year, until at present a true congestion exists there in winter, which is little relieved even on occasions of heavy snow storms. The deer of this particular locality no longer desert the 4000 foot altitude when food plants are deeply buried, because they have come to regard the "back-door hand-outs" of Yosemite villagers as a reliable food supply. As a matter of fact, they partake of quantities of garbage at all times, regardless of snow depth, and persistent feeding in this manner, together with the general let-down in vigilance resulting from continued life among human residents, has made of them a sodden group, which contrasts greatly with the graceful alertness of the normal animals not so closely associated with human affairs. It should be remembered, however, that the several hundred deer of such modified habits represent less than one per cent of the total deer population of the park.

Grinnell and Storer (1924) found that winter range extended westward from Yosemite National Park to include regions as low as 1500 feet. The Yosemite map (Fig. 3) shows clearly the relationship of winter range to the park area but is not large enough to include all winter range known to be available in the region. Conditions within much of the winter area west of Yosemite are typical of the Upper Sonoran Zone. Chaparral, including such species as mountain mahogany, *Cercocarpus parvifolius*; western red bud, *Cercis occidentalis*; poison oak, *Rhus diversiloba*; California buckeye, *Aesculus californica*; manzanita, *Arctostaphylos mariposa*; sagebrush, *Artemisia tridentata*; and wedgeleaf ceanothus, *Ceanothus cuneatus*, covers the dry rolling prominences or blankets the precipitous canyon sides. Ample cover is provided by this dwarfed forest, and except in regions overrun by stock, affords an abundant food supply. The digger pine, *Pinus sabiniana*, and the interior live oak, *Quercus wislizenii*, make a feeble show at foresting the region.

As long as snow conditions permit, many of the deer do not enter deeply into this belt but remain near the edge of the Transition Zone, where they occupy the yellow pine forest (*Pinus ponderosa*) and feed on their favorite browse, the deer brush, *Ceanothus integerrimus*. Upper limits of winter range are clearly defined by snow depth. If a period of mild weather causes shrinkage of the snow cover, deer immediately take advantage of the opportunity to move into the heart of the Transition Zone. Winters at middle alti-

tudes in the Sierras are not infrequently mild, but it should not be understood that regions above 5500 feet are commonly free from snow during winter months. Up to this limit (5500 feet), however, deer may be found whenever snow conditions permit.

The winter range of mule deer inhabiting eastern slopes of the Sierra in the Yosemite region differs greatly from that described for the western slope. It occupies mountainous country 7000 feet to 8000 feet above sea level and experiences winter conditions of a severity to be compared with that of the Yellowstone country. The limits of this range indicated on the accompanying map have been supplied by Supervisor Roy Boothe of the Inyo National Forest and Supervisor W. M. Maule of the Mono National Forest.

Mr. Maule, writing me under date of Nov. 7, 1930, states:

"It is quite evident that the summer range of these deer extends some miles over the Sierra summit to the west and the line dividing summer and winter range is roughly that of the merging of the single-leaf pine with the Jeffrey pine. This line, of course, is primarily determined by climatic conditions which affect the peculiar vegetative types. There is an intermediate zone lying partly within the two types in which the deer winter and this occupied area varies with the character of the winter, passing farther eastward during periods of heavy snowfall.

"Within the area I have indicated as winter range (See Fig. 3), one finds tracts of high mountains whose midwinter snows force the deer to lower altitudes where the living conditions are more acceptable or possible. Within this winter area, also, the deer are required to compete with quite a population of sheep which graze over the more accessible portions while the deer are restricted to the more rugged canyons or are held to certain timbered areas which offer them forage which is not relished by the sheep. This latter includes the nuts of single-leaf pine and mountain mahogany twigs.

"I have frequently found cases where deer have "yarded" among thickets of bitter brush, *Kunzia tridentata*; it seems that these instances have been due largely to the deer having been caught in heavy storms and were unable to find their way to the more snow-free areas."

BREEDING

Evidences of the rut are first to be observed among the animals on winter range. Breeding dates have already been given under "Rearing of Young." Without exception, the earliest breeding activity was noted to occur among those animals which had spent the summer at low levels, or among the first arrivals from summer range. Some breeding takes place among deer enroute to winter range, but I have never seen evidence of the rut in animals that had not descended below the heart of summer range.

The breeding activity in Yosemite is in every way similar to that in the Yellowstone, except that it occurs three weeks or a month later. In general, it may be said that this is consistent with the later dates of fall migration in Yosemite. The mad racing of both sexes at this time is quite as described for the Yellowstone region, and further account of breeding affairs would but

repeat what has already been stated. One note relative to the age at which bucks manifest the breeding instinct seems worthy of place here and is quoted from my Yosemite notebook:

"Jan. 2, 1925. At 8:00 a. m. I went to old Camp Lost Arrow to make observations on breeding deer. I found the animals still very active and was especially impressed by a little buck with spikes not more than four inches long. He appeared to be beside himself with the mating desire and determined to secure an eligible doe that was attended by a six-point buck. When the young buck would approach the doe, he was immediately chased away by the big buck, and for one and one-half hours the older animal was kept in a state of distraction. Such mischievousness, however, was not the youngster's main objective. It was evident that in spite of his age (he could not have been more than eighteen months old), he was ready to breed. Finally, after many attempts to get close to the active doe, he humped his back and projected his penis some six or seven inches from its sheath. It moved spasmodically, dorso-ventrally, a few times, after which the buck turned his head and licked the organ with his tongue. It then disappeared. There was no evidence of an emission."

It is likely that such sexual activity in so young a buck was an instance of precocity, for at no other time were very young males noted to manifest so evident an urge to breed.

FOOD HABITS

As has been pointed out, the west slope Transition and Upper Sonoran Zones in which Yosemite deer winter do not experience extremes of temperature or heavy snowfall, which characterize the severe winters in the Yellowstone. Sub-zero temperatures are unusual, and daily mean temperatures of less than 35° F. are unknown. Days of warm sunshine prevail, and snow accumulates to no great depth. Food plants are present in abundance and in a palatable condition. Cover is ideal, and few enemies exist. The hunting season extends from September 16 to October 15 and comes at a time when the great part of the Yosemite animals are safe within the limits of the park. In general, it may be said that winter range adjacent to the park, in its present condition, is a veritable deer paradise. Possibility of serious change in the existing favorable conditions (Brown, 1929, ms.) constitutes sufficient reason for extending the park boundaries to include winter range.

Food plants known to be eaten are: *Arctostaphylos mariposa*, Mariposa manzanita; *Artemisia vulgaris*, sage brush; *Ceanothus cuneatus*, buck brush; *C. integerrimus*, deer brush; *Cercocarpus parvifolius*, mountain mahogany; *Cirsium californicum*, Sierra thistle; *Cornus californica*, creek dogwood; *C. Nuttallii*, mountain dogwood; *Erigeron canadensis* (eastern United States) and *E. virgatum*, horseweeds; *Festuca elatior*, meadow fescue grass; *Garrya fremontii*, bear brush; *Holcus lanatus*, velvet grass; *Libocedrus decurrens*, incense cedar; *Lotus americana*, Spanish clover; *Oenothera hookeri*, evening

primrose; *Phoradendron villosum*, common mistletoe; *Populus trichocarpa*, black cottonwood; *Prunus demissa*, western chokecherry; *P. subcordata*, Sierra plum; *Pteris aquilina*, common brake; *Quercus chrysolepis* (also acorns), canon oak; *Q. kelloggii* (also acorns), California black oak; *Q. wislizenii*, interior live oak; *Rhamnus californica*, coffee berry; *Ribes quercetorum*, gooseberry; *Rosa californica*, California wild rose; *Rubus leucodermis*, wild raspberry; *Rumex acetosella* (European), sheep sorrel; *Salix lasiandra*, yellow willow; *Sambucus velutina*, elderberry; *Symphoricarpos racemosus*, snow berry; and *Umbellularia californica*, California laurel.

Of these, the following are of greatest importance because of their occurrence in quantity and their apparently greater relative palatability: *Arctostaphylos mariposa*, *Ceanothus cuneatus*, *Ceanothus integerrimus*, *Cornus californica*, *Festuca* sp., *Libocedrus decurrens*, *Prunus demissa*, *Quercus chrysolepis*, *Q. kelloggii*, *Rosa californica*, and *Salix* sp.

It is seldom that the snow cover of the 3000 to 4000 foot belt persists after March 1. As has been explained, a great number of the animals stay in close proximity to the snow line through the winter months and with rapid shrinking of the snow in the spring make their way upward, keeping pace with the retreat of snow. Above 6000 feet, climatic conditions are such that the melting of snow is retarded, and regions above this level are seldom free from snow before May 1. As a consequence, the deer may leave winter range but do not at once succeed in occupying summer range. They are present in numbers in the zone between 4000 and 6000 feet during the months of March and April. In this respect, the spring migration in Yosemite differs notably from the same movement in the Yellowstone region, where because of food advantages, the deer remain on winter range for some six weeks after the zone immediately above winter range is free from snow. The explanation seems to lie in the fact that the Yosemite plants of the middle altitudes leap into the spring state with a rapidity not possible under Yellowstone conditions. Grasses and other herbaceous plants produce green shoots immediately after snow melts. Some of them remain green all winter and take an important place in the winter diet. *Arctostaphylos mariposa* and *Ceanothus cuneatus* sometimes burst into bloom while surrounded by snow.

SPRING MIGRATION

The favorable state of forage plants having induced the deer to ascend with the upward retreat of the snow line, the first of May usually finds a considerable deer population in regions as high as 6000 feet. Above this level, snow does not disappear so rapidly, and when it does melt, low temperatures prevail which serve to retard plant development. As a consequence, deer do not rush into the area as they did when occupying the 4000 to 6000 foot zone. In this stage of the upward movement, the features of spring migration are much like the Yellowstone spring drift. Deer remain at those levels where

palatable food is most abundant and, when spring conditions have affected higher regions, they travel upward at a deliberate rate which fairly keeps pace with the development of plants. Routes are the same as those followed in the downward drift.

Arrival in the heart of summer range (7500 ft.) is usually three weeks or a month after the greater part of the snow of that level has disappeared. By this time (June 1 to 15), forage has attained a state of development attractive to the animals, and they enter upon the normal existence of summer. Those individuals that seek higher feeding grounds (more bucks than does) succeed in reaching the upper limits of summer range (9000 ft.) two or three weeks (July 1 to 15) after arrival on the 7500 foot level.

The spring molt occurs in May. No instance of a Yosemite deer arriving on summer range in the winter coat of "blue" has come to my notice.

A unique opportunity to study the seasonal movements of a mule deer of the Sierras was provided when a bell was placed on a Yosemite doe. (Russell, 1925). For nearly a decade, this animal was under observation and provided definite evidence as to what constitutes a migration route. It has been generally assumed by the inhabitants of the Sierras that deer regularly follow the same route year after year and consistently occupy the same range. In this instance, that belief has been substantiated so far as concerns the route of travel. The doe in question has always wintered in the Merced Canyon at Cascades (3500 ft.) or Yosemite Valley (4000 ft.). During the first years that she was under observation, her summers were spent in Little Yosemite Valley (6200 ft.), but in 1929 she was seen to ascend the Merced to its very headwaters and spent at least a part of the summer near the summit (10,000 ft.) of the range. On that occasion, she was not accompanied by fawns, as was always the case during her summers in Little Yosemite. The maximum distance traveled was about forty miles, with an altitudinal change of 6500 feet. While the destination at either end of the journey varied, this doe did not show an inclination to leave the Merced drainage system. In fact, her route was invariably the same between Cascades and Washburn Lake, a distance of about twenty-five miles. This is to be expected since the most accessible route is here much limited by the canyon of the Merced.

Mountaineers, generally, maintain that deer do not pass from one drainage system to another. After the destruction of the "Tuolumne Herd," because of foot and mouth disease in 1925-1926, it was hoped by some officials that deer from the adjacent Merced drainage system would repopulate the Tuolumne region of the park. No evidence of such a movement of deer could be noted. In 1929 and 1930, deer from the Merced drainage basin were captured and transported to the Tuolumne. What the seasonal movements of the transplanted animals may have been has not been observed.

Excellent opportunities exist in both Yellowstone and Yosemite to carry

on marking experiments and so accumulate more evidence regarding migration routes, speed of travel during migration, and home territory. The organization of the system of general ecological studies in the national parks which is now contemplated should embrace such experiments.

DISCUSSION

RELATION OF SEASONAL MOVEMENT TO BREEDING ACTIVITIES

Accumulated evidence presented (pp. 12, 29) points to the conclusion that in both the Yellowstone and Yosemite regions, breeding does not take place among migrants while they are on summer range. In the geyser basin region of Yellowstone, where some deer do not migrate, breeding occurs at high levels generally regarded as summer range. Breeding in the Yosemite country usually occurs two weeks later than in the Yellowstone region, and in both sections the earliest breeding takes place at the lower levels. As the season progresses, some animals enroute to the winter range may show evidences of the rut, but by far the greater number of deer reach winter range before becoming sexually active. It may be stated that breeding is coincident with arrival on winter range. Since nonmigrants of the geyser basins on the high plateau of Yellowstone Park breed at normal dates, no evidence can be produced showing breeding to be a causative factor in the seasonal movement.

RELATION OF MIGRATION TO BIRTH OF YOUNG

In Yellowstone Park, fawns are born in June or early July. Does heavy with young make the journey to summer range with other migrants and arrive there a few days or a few weeks, according to the season, prior to birth of the young. The Yosemite breeding dates tend to average from a few days to two weeks later than the Yellowstone dates, and birth of young is slightly later accordingly (p. 20). The period of gestation is ordinarily regarded to be seven months. Hall (1927) gives it as six and one-half or seven months. Migrating does of Yosemite National Park arrive on summer range but a few days or a few weeks before giving birth to young.

The question may arise, "Do does seek higher levels in order that their young may benefit by certain favorable conditions of the upper zone?" I think this may be answered in the negative, as no evidence exists indicating that Canadian and Hudsonian conditions offer anything advantageous to fawns. In the Yellowstone, elk sometimes descend to lower levels to give birth to young and, when the calves are strong enough, return to summer range. This habit has not been observed among the deer, but such behavior of elk indicates that summer range offers no particular advantages to the very young of either animal.

Fawns born at 4000 feet or lower evidently do not migrate. Fawns born on any part of the true summer range accompany the mothers all summer and

are escorted by them to winter range in the fall. It is usual for the family group to remain together through the winter (except for possible separation during a few days at the time of the mother's breeding period) and, as a group, to make the ascent to summer range the next spring. Upon the arrival of a new family, the yearlings are driven away by the mother.

A nice correlation exists between birth of young, rearing of young, and seasonal migration, but only in so far as it is a fact that the young are shown the routes of travel by the experienced mother can the relationship be shown to be of a causative nature.

RELATION OF MIGRATION TO CLIMATOLOGICAL PHENOMENA. TEMPERATURE

In both regions, the upper limits of summer range (Yosemite, 9000 ft.; Yellowstone, 8500 ft.; see Figs. 4, 5) experience mean temperatures of 30° to 40° F., with minimum temperatures of 5° to 20° F. quite usual. Deer of these high levels react to the drop in temperature, or to the change in food plants which results from the low temperature, and manifest a tendency to move to lower parts of the summer range. This is the beginning of the fall migration, and in the Yosemite country, it may precede snow storms by as much as two months. In the Yellowstone region, it may or may not precede snow storms (p. 11). September snow storms in that part of the Rocky Mountains are not unusual, and the first fall movements of deer of high levels are usually coincident with snow fall.

Minimum temperatures of 32° F. result in marked changes, external and internal, in forage plants. To what degree this change in forage conditions is responsible for the first movements of the deer of high levels cannot be determined, but very evidently a correlation exists.

In the middle regions of summer range, initial fall movements (one exception during the course of this study, p. 24) are delayed in spite of drops in temperature and changes in food plants, until snow storms occur.

In comparing daily mean temperatures of the Yellowstone central winter range (6200 ft.) at the time of the beginning of the spring migration (Figs. 4, 5), one finds that mean temperatures vary from 37° to 47° F. (1928, 45°; 1929, 37°; 1930, 47°; see Table II). Mean temperatures of the central summer range at the time of beginning of the fall migrations vary from 24° to 31° F. (1928, 24°; 1929, 31°; 1930, 28°). In the spring, daily mean temperatures of the summer range at the time of arrival of deer vary from 41° to 45° F., and in the fall, mean temperatures of the Yellowstone central winter range vary from 16° to 23° F. Comparison of these data with similar data for the Yosemite region (Table II) indicates that mean temperatures at times of migration vary much as they do in the Yellowstone country, but that higher temperatures prevail in the Sierras when migrations take place.

TABLE II. Comparison of Daily Mean Temperatures at Times of Deer Migrations Figures indicate the mean temperature in degrees Fahrenheit at the time of arrival of deer at 6500 and 7800, or 4000 and 7000 foot levels, and of departure at the 6200 or 3000 foot levels.

YELLOWSTONE								
Elevation	Spring Migration				Fall Migration			
		1928	1929	1930		1928	1929	1930
6200'		45°	37°	47°		22°	23°	16°
6500'		45°	36°	42°		17°	27°	21°
7800'		45°	39°	41°		24°	31°	28°

YOSEMITE								
Elevation	Spring Migration				Fall Migration			
	1927	1928	1929		1927	1928	1929	
3000'	58°	62°	53°		42°	51°	47°	
4000'	59°	63°	57°		40°	48°	45°	
7000'	53°	54°	46°		42°	38°	43°	

SNOWFALL

Early snow storms have a marked effect on deer on summer range (Figs. 4, 5). In Yellowstone, the central plateau region experiences freezing temperatures in September, and animals manifest a restlessness at this time which results in indefinite extension of daily movements. A notable number of animals begin their travel toward winter range when the first snow storms occur. These first movements may carry the animals slowly over a route of some twenty to fifty miles, all of which may be at levels regarded as summer range, but actual descent of the greater number is delayed until the coming of severe storms in November. These later severe storms are decisive factors in the fall movement.

In Yosemite National Park, those animals of the upper limits of summer range (9000 ft.) may respond to some undetermined stimuli other than snow and begin their migration in advance of fall storms. The large part of the deer population in the heart of summer range (7500 ft.) shows no great inclination to travel until snow storms occur (p. 25). Even here, the migration is not a positive descent but rather an indefinite movement which tends to carry the animals to areas of little snow. Here, many will linger until heavy snows cause them to descend with a rush to true winter range (p. 27).

In both Yosemite and Yellowstone, severe snow storms are decisive in causing the deer wholly to desert their summer range.

DEPTH OF SNOW

Snow is commonly present on the Yellowstone winter range to a depth of five to fifteen inches. The animals of that region regularly contend with this snow cover from November to March. Much of the Yosemite winter range is below the snow line, and the higher sections of it seldom are covered to a depth of more than five inches (Figs. 4, 5). One or two inches is the usual snow cover here, and there are numerous areas where this small amount of snow melts nearly as fast as it falls. The usual period of snow is four months, as against five in the Yellowstone country.

In comparing the winter behavior of deer in Yellowstone and Yosemite, the writer emphasizes the fact that the Yellowstone animals are taxed with rigorous winter conditions, while the Yosemite animals enjoy comparatively mild weather. Depth of snow, unquestionably, affects the choice of winter range by deer in both regions. The Yellowstone animals of the present seem content with conditions that prevail. Only in years of excessive snowfall, such as occurred in 1910-1911, 1916-1917, 1919-1920, 1921-1922 (Fletcher, 1928) do the deer make a considerable effort to leave the protecting limits of the park. Grinnell and Storer (1924) state that deer cannot feed in snow of greater depth than eighteen inches. In the years mentioned, twenty-four to thirty-six inches of snow covered the normal winter range of the Yellowstone deer. On these occasions, both elk and deer attempted to travel from the park to the lower areas along the Yellowstone River (the winter range of primitive times) and were slaughtered by hunters or died in great numbers from starvation (Rush, 1929, 1930). The ever impending danger of disastrous loss from the causes described has led to national interest in the Yellowstone game herds, and a splendid start has been made in acquiring control of lands north of the park boundary in order that winter range may be extended when severe winters demand it.

In Yosemite National Park, the winter range situation is quite as deserving of study as is the Yellowstone problem. The most cursory examination of the accompanying map (Fig. 3) shows that the park affords all-year protection for no more than five per cent of the deer which in summer reside within the park. Present conditions constitute no great menace (p. 30), but it is impossible to offer assurance that the future may not hold a situation which will constitute a catastrophe for the deer herds. In 1930, a beginning was made by extending the western boundary of the park. 7,725.19 acres, valued at \$3,300,000 were added in the vicinity of Ackerson Meadow, Tuolumne Grove, and the Merced Grove (Albright, 1930).

RELATION OF WEATHER PHENOMENA TO FOOD SUPPLY

In both Yellowstone and Yosemite, the summer diet of deer is characterized by an abundance of succulent herbage with a proportion of woody matter,

such as twigs, bark, and roots, which by bulk may constitute a fifth to a third of the whole. Contents of the few stomachs examined (three in Yellowstone; five in Yosemite) indicate no marked difference in the general nature of summer food for the two regions.

Consistent with the great difference in winter weather conditions for the two localities is the general tendency for the nature of winter food to differ. In Yellowstone, stomachs of deer killed in winter commonly contain eighty per cent or more of woody material, and the remainder is made up of dried grasses and leaves. Most of the Yosemite animals (19 stomachs examined), even in winter, succeed in securing some fifty per cent of their food, by bulk, in green succulent or semi-dried form.

These differences result from the fact that most of the Yosemite winter range lies within a belt in which mild winter conditions permit of continued physiological activity in many plants. Grasses and many other herbaceous plants of the lower Yosemite country are green throughout the winter. At this time, the deer of that region partake of a far greater percentage of grass than is ordinarily recorded by most observers. In contrast with this are the severe winter conditions of all of the Yellowstone region, which bring about complete autumnal changes in forage plants. Yet, deer partake of the woody parts of plants and dried vegetation and, with artificial feeding of hay to supplement this forage, suffer no great loss in ordinary winters (Haberlandt, 1915).

In brief, it is to be concluded that low temperatures, while bringing about a great physical change in forage plants, do not render them unfit for food. Deer could safely reside in winter at high levels in the mountains so far as concerns the food value of high mountain plants. Low temperatures, then, are not the determining factor in fall deer migration.

Deep snow, while it in no way affects the food value of the plants themselves, does effectively render them inaccessible to deer. In this role, it becomes, preëminently, the causative factor in bringing about the fall movement of deer (pp. 11, 27). The spring movement hinges upon two factors in weather phenomena: temperature and snow depth (pp. 16, 31). Although dead plants of the summer range may in the spring become accessible because of the melting of the snow, upward movement of deer does not keep pace with the disappearing snow. The true spring migration awaits the development of new plant growth, and this development is correlated with moderation of temperatures.

HABIT AS A FACTOR IN MIGRATION

Fawns accompany their mothers in making their first migration from summer to winter range. In many instances, too, the young accompany the does in the succeeding journey from winter to summer range. Thus, the

habit of following certain routes of travel, as well as the habit of moving from one range to another, may be founded in individual animals.

Some evidence is found that development of forage controls the spring use of certain migration routes (p. 16), but because deer of a winter locality which is served by more than one route of travel divide in the spring and make use of all routes regardless of development of forage, it is concluded that habit is an important determinant in the choice of migration lanes. In the Sierras, regular use of routes within single drainage systems has served to restrict deer to ancestral summer and winter homes.

Observations made in Yellowstone and Yosemite upon individual deer with natural characters which permit of their identification have provided data upon routes followed (pp. 17, 32). These studies over a period of years reveal that the individual animals habitually follow the same routes of travel. In the Upper Yellowstone-Thorofare region, deer are known to cross the Absarokas, a major divide, in moving from winter to summer range, and vice versa. This instance of failure to follow a single drainage system when migrating indicates that repetition of unusual movements may establish migration habits of an irregular nature.

POSSIBLE INFLUENCE OF SEASONAL PHYSIOLOGICAL RHYTHM

There is a well-marked and nicely correlated seasonal rhythm of breeding, rearing of young, and migration in the mule deer. Feeding habits and migration are closely related to the prevailing environmental complex, and the seasonal movements are controlled by environmental factors. However, the fall restlessness frequently manifested by deer of the Yosemite high country in advance of marked climatological changes seems to indicate a lack of physiological balance and suggests the possibility that a seasonal physiological rhythm may be the underlying cause of the migration. Such a relationship perhaps is the basis of the migration phenomena, but the time of seasonal movements is evidently controlled by environmental factors.

SUMMARY

1. The mule deer of the Yellowstone and Yosemite regions occupy distinct summer and winter ranges. In the spring, they move from the winter range to the higher summer range. In the fall, they reverse this movement. Routes followed are from ten to sixty miles in length.

2. Mating behavior and the birth of young are correlated with the seasonal migration, but apparently no causative relationship exists between these life activities and the migration phenomena.

3. Drops in temperature and early fall snow storms are coincident with a restlessness among deer of the upper summer range, and the fall movement begins with the descent of these animals from the higher levels. Daily mean

temperatures at the time of migration vary from year to year. Mean temperatures of the Yellowstone region are 10° to 20° F. lower than those of similar levels in the Sierras during the migration period.

4. Heavy snow storms are the decisive factor in the fall migration of deer in all parts of the summer range.

5. Dates of snow disappearance control the spring migration only so far as the melting of snow is related to temperatures conducive to plant growth. The spring migration may be delayed for weeks after snow has disappeared from the summer range. Development of forage plants is dependent upon temperature, and the time of spring migration is dependent upon forage conditions.

6. If suitable food is available in a given area throughout the year, some or all of the deer of that area may not migrate. If desirable food becomes limited or inaccessible at some seasons, migrations result and these take the animals to other areas offering an adequate food supply. Availability of desirable food is the most important controlling factor in determining range to be occupied by deer at all times.

7. Evidence suggests that habit is most important in determining the exact migration route followed.

8. A seasonal physiological rhythm may possibly be the underlying cause of the seasonal movements, but availability of food evidently controls the time of migration.

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FIG. 1. Winter Range of Mule Deer of the Yellowstone Park Region.

In general, migration routes follow drainage systems. An interesting exception is found in the Upper Yellowstone country, where deer move out of the Yellowstone Valley, cross the Absarokas, and descend to winter range on the Shoshone River.

By far the greater number of deer that occupy the Yellowstone Park plateau (7800 ft.) in summer descend to regions below 7000 feet in winter. Many descend to 5000 feet altitude. Certain deer are known to spend the summer near Thumb (7800 ft.) and the winter at Mammoth (6200 ft.). The route between these two ranges is some sixty miles long. The deer of the Old Faithful-Madison Junction area (7500 ft.) occupy the same range winter and summer. These examples of non-migrants provide an interesting control on the observations and conclusions upon which a part of this paper is based.

MANY PARALLEL TRAILS IN A CANYON USED BY MIGRATING DEER

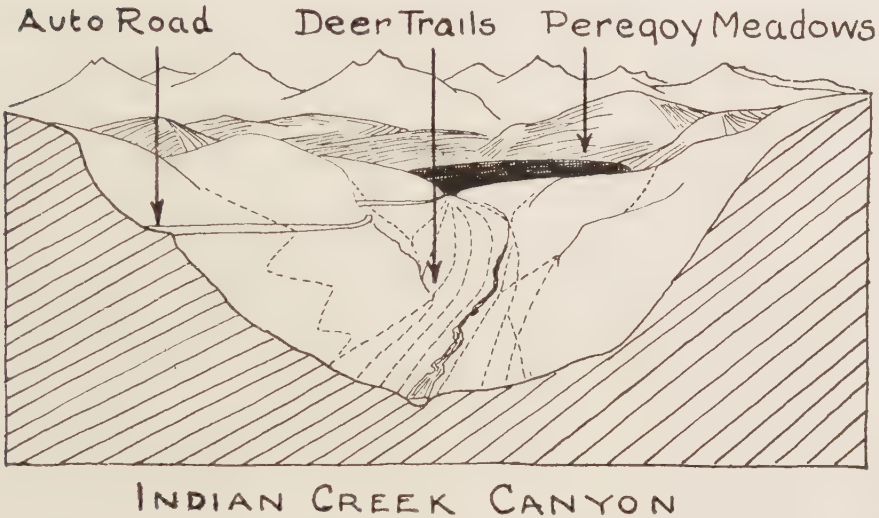


FIG. 2. During the course of a movement of deer in the Yosemite region, certain canyons are noted migration routes. In such canyons, parallel trails are numerous, and the general appearance of the canyon floor suggests the presence of great numbers of deer. This "used" appearance is obliterated in the fall by snowfall. The spring movement again leaves its marks upon the canyon, but these evidences are soon wiped out by rains and the growth of plants. Perhaps, but one trail will be conspicuous through the summer. This single trail is used by the comparatively small number of animals that are the summer occupants of the immediate locality.

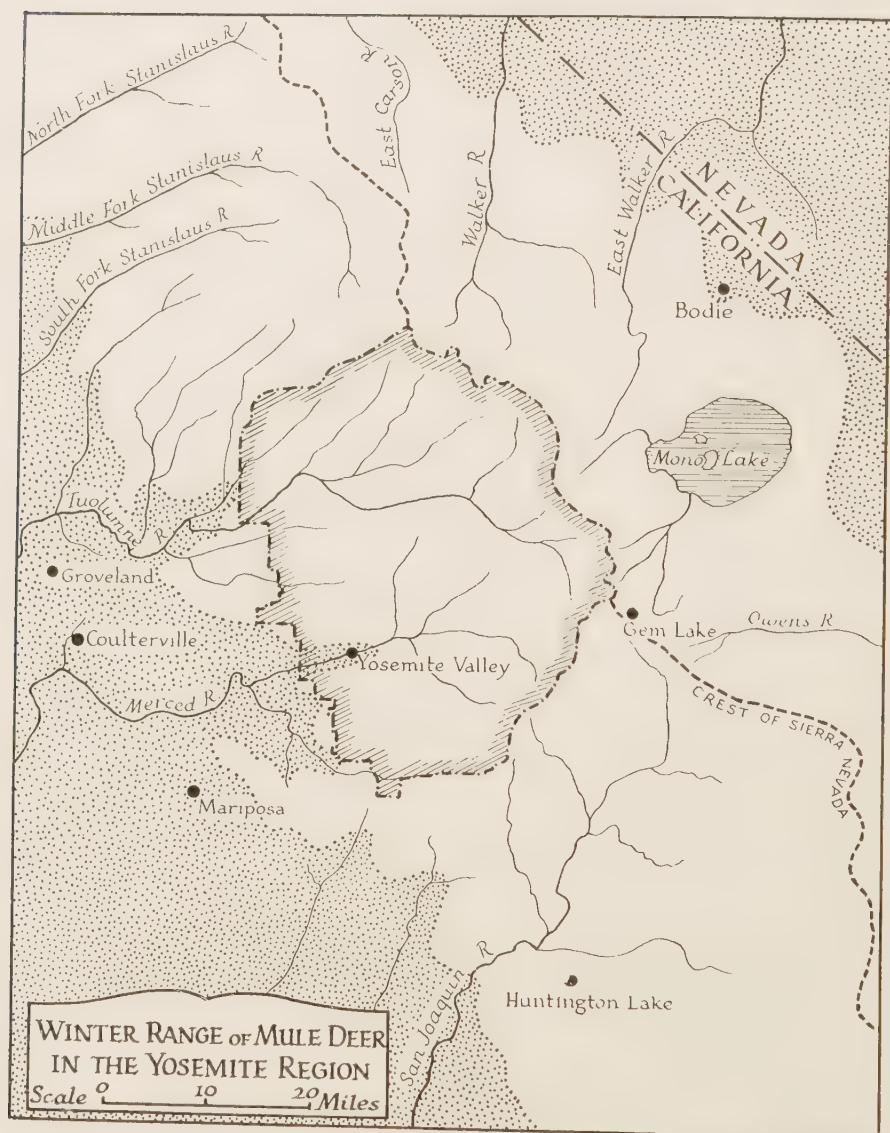


FIG. 3. Winter Range of Mule Deer in the Yosemite Region.

The deer which in summer densely populate the Yosemite National Park are caused to move out of the park when snow falls. They move from their summer haunts (6500 ft. to 9000 ft.) along the stream courses of the west slope of the Sierras to the regions of mild climate in the chaparral and yellow pine belts of 1500 feet to 5000 feet altitude. Immediately east of Yosemite National Park, mule deer live under conditions that differ widely from the situations of the west slope. The animals of the east slope winter in areas 7000 feet to 8000 feet above sea level and experience conditions to be compared with the severe winters of the Yellowstone Park country. Deer of both slopes parallel stream courses when making their seasonal movements and tend to remain in the same drainage systems throughout their lives.

CORRELATION OF DEER MOVEMENTS WITH PERIODIC PHENOMENA OF YELLOWSTONE 1928

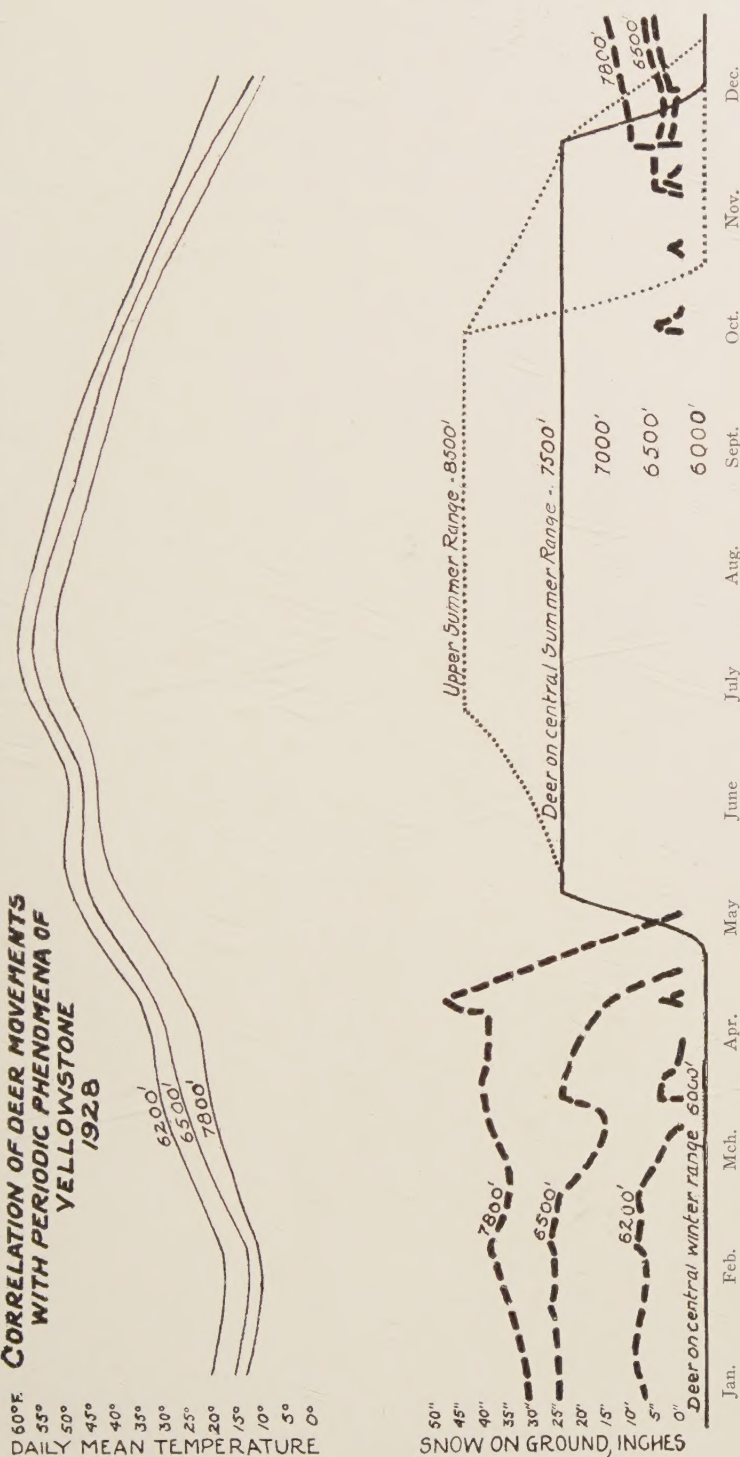


Fig. 4. Deer Movements and Climatological Phenomena; Yellowstone National Park, 1928.

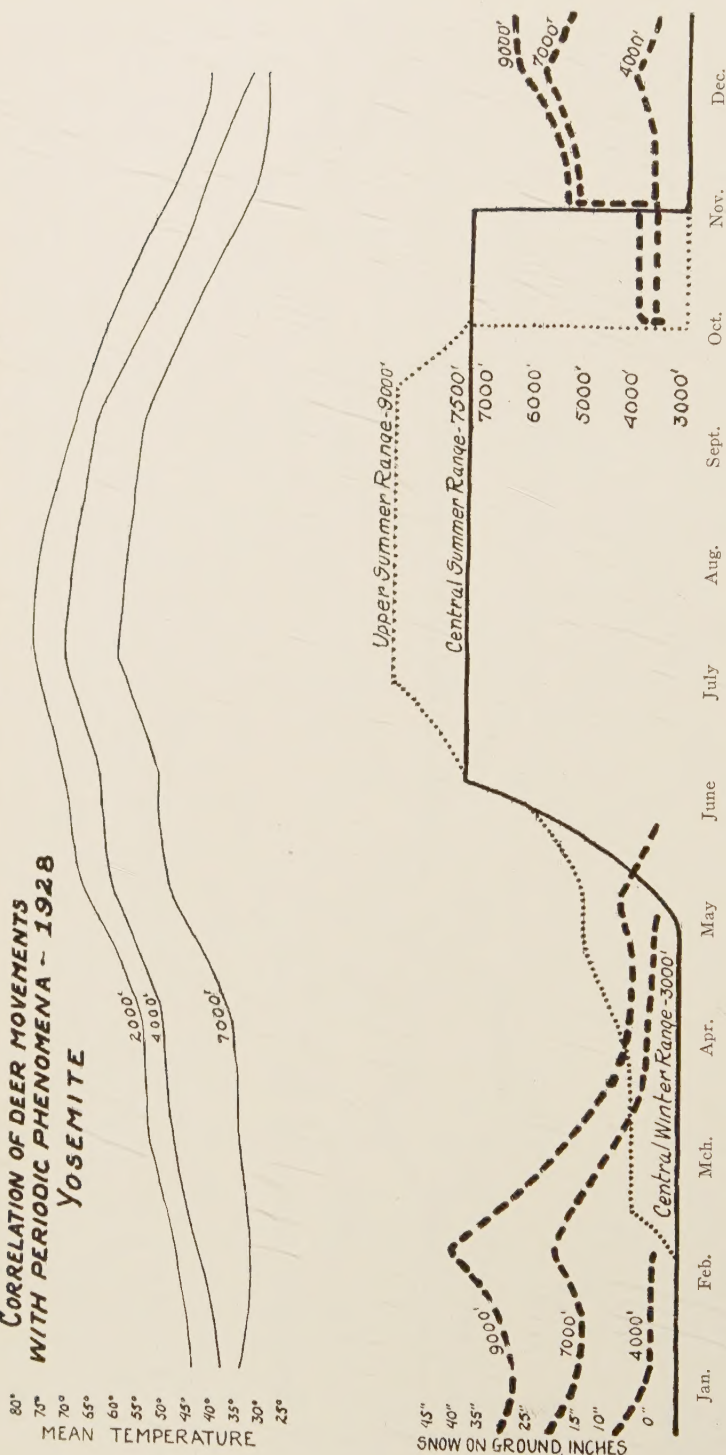
Climatological observations were recorded at Mammoth Hot Springs (6200 ft.), Buffalo Ranch (6500 ft.), and Lake (7800 ft.). Data supplied by the Yellowstone Park Office of the U. S. Weather Bureau.

The deer movements are indicated by solid and dotted lines. The solid line shows altitudinal location of the majority of the animals. The dotted line indicates the movements of a minor number. Snow depth is represented by the heavy broken line. The snow of the central winter range (6000 ft.) disappeared on April 10. The deer made no movement away from winter range for twenty-two days after the ground was clear. The ascent then (May 5) was steady, and ten days later (May 15) the greater number of the animals were upon the central plateau. The snow line, at this time, was at about the 7800 foot level. The deer remained on summer range for six and one-half months. A snow storm on October 10 started the downward drift of some of those at the upper limits of summer range (8500 ft.). The great majority, however, remained on summer range until the severe snow storm on November 29. Many of these animals were fifty or sixty miles distant from and 1500 feet or 2000 feet above winter range. The journey to winter range frequently took a week or ten days to accomplish.

Analysis: Yellowstone deer do not follow the retreating snow line in the spring. The upward drift is delayed three weeks or a month after snow disappears from winter range. During this time, spring progresses up the mountainsides, and by the time true spring migration is under way, forage plants of summer range have attained the spring condition. The fall movement was initiated by a snow storm, and the decisive stimulus which took all deer to winter range was a severe snow storm.

FIG. 5. Deer Movements and Climatological Phenomena; Yosemite National Park, 1928.

CORRELATION OF DEER MOVEMENTS WITH PERIODIC PHENOMENA - 1928 YOSEMITE



Climatological observations were recorded at Sonora (2000 ft.), Yosemite Valley (4000 ft.), Huntington Lake (7000 ft.), and Gem Lake (9000 ft.). See map.

The deer movement is indicated by solid and dotted lines. The solid line shows altitudinal location of the majority of the animals. The dotted line indicates the movements of a minor number. Snow depth is represented by the heavy broken line.

Snow disappeared at the 4000 foot level on February 15. Deer immediately moved up with the retreating snow line. No ascent above the 6000 foot level was made prior to June 7. The 7000 foot level on February 15. It was not until a month later (June 16) that this level was occupied by deer. During the interim, vegetation of that level (7000 ft.) attained the spring state. Most of the snow disappeared on the 9000 foot level on June 5. Deer did not attain those heights until July 13. This year the animals remained on summer range for about five months. The earliest downward drift occurred among the comparatively small number in the upper limits of summer range (9000 ft.). Here, the fall preceded snow storms by two weeks. On October 11 several inches of snow fell upon all of the summer range. A decided migration took place during this storm, and many animals arrived on winter range at this time. A greater number, however, remained at 7000 feet in spite of the inch or two of snow, and it was not until the heavy snow of November 10 (18 in. at 7000 ft.) that all of the deer hurriedly left the summer range and occupied true winter range.

Analysis of these data points to the fact that the spring migration up to 6000 feet was controlled by the melting of the snow cover. Above 6000 feet, the movement was delayed about thirty days after the disappearance of snow, during which delay forage plants up to the 7500 foot level attained the spring state. The fall movement of deer in the upper limits of summer range (9000 ft.) began without the impetus of snow storms. In the regions of summer range in which deer were present in greatest numbers (about 7500 ft.), the migration was initiated by snow storms.

